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Review article

Neural correlates of emotion-attention interactions: From perception, learning, and memory to social cognition, individual differences, and training interventions



Florin Dolcos^{a,b,*}, Yuta Katsumi^{a,b}, Matthew Moore^{a,b}, Nick Berggren^c, Beatrice de Gelder^d, Nazanin Derakshan^c, Alfons O. Hamm^e, Ernst H.W. Koster^f, Cecile D. Ladouceur^g, Hadas Okon-Singer^h, Alan J. Pegnaⁱ, Thalia Richter^h, Susanne Schweizer^j, Jan Van den Stock^k, Carlos Ventura-Bort^l, Mathias Weymar^l, Sanda Dolcos^{a,b,*}

^a Department of Psychology, University of Illinois at Urbana-Champaign, Champaign, IL, USA

^b Beckman Institute for Advanced Science & Technology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

^c Department of Psychological Sciences, Birkbeck, University of London, London, England, United Kingdom

^d Department of Psychology and Neuroscience, Maastricht University, Maastricht, Netherlands

^e Department of Biological and Clinical Psychology/Psychotherapy, University of Greifswald, Greifswald, Germany

^f Department of Experimental-Clinical and Health Psychology, Ghent University, Ghent, Belgium

^g Department of Psychiatry, Western Psychiatric Institute and Clinic, University of Pittsburgh Medical Center, University of Pittsburgh, Pittsburgh, PA, USA

^h Department of Psychology, University of Haifa, Haifa, Israel

ⁱ School of Psychology, University of Queensland, Saint Lucia, Queensland, Australia

^j Institute of Cognitive Neuroscience (Developmental Cognitive Neuroscience Group), University College London, London, England, United Kingdom

^k Laboratory for Translational Neuropsychiatry, Research Group Psychiatry, Department of Neurosciences, KU Leuven, Leuven, Belgium

^l Department of Psychology, University of Potsdam, Potsdam, Germany

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ABSTRACT

Due to their ability to capture attention, emotional stimuli tend to benefit from enhanced perceptual processing, which can be helpful when such stimuli are task-relevant but hindering when they are task-irrelevant. Altered emotion-attention interactions have been associated with symptoms of affective disturbances, and emerging research focuses on improving emotion-attention interactions to prevent or treat affective disorders. In line with the *Human Affectome Project's* emphasis on linguistic components, we also analyzed the language used to describe attention-related aspects of emotion, and highlighted terms related to domains such as conscious awareness, motivational effects of attention, social attention, and emotion regulation. These terms were discussed within a broader review of available evidence regarding the neural correlates of (1) *Emotion-Attention Interactions in Perception*, (2) *Emotion-Attention Interactions in Learning and Memory*, (3) *Individual Differences in Emotion-Attention Interactions*, and (4) *Training and Interventions to Optimize Emotion-Attention Interactions*. This comprehensive approach enabled an integrative overview of the current knowledge regarding the mechanisms of emotion-attention interactions at multiple levels of analysis, and identification of emerging directions for future investigations.

Abbreviations: ABC, arousal-biased competition; ABM, attentional bias modification; ACC, anterior cingulate cortex; ACT, attentional control theory; AMs, autobiographical memories; AMY, amygdala; BA, Brodmann area; CS, conditioned stimulus; DES, dorsal executive system; dlPFC, dorsolateral prefrontal cortex; Dm, Difference due to memory; EBA, extra-striate body area; EEG, electroencephalography; EM, episodic memory; ERP, event-related potentials; FA, focused attention; FBA, fusiform body area; FFA, fusiform face area; FG, fusiform gyrus; fMRI, functional magnetic resonance imaging; HC, hippocampus; IPL, inferior parietal lobule; IPS, intraparietal sulcus; LPC, lateral parietal cortex; LPP, late positive potential; MEG, magnetoencephalography; mPFC, medial prefrontal cortex; MTL, medial temporal lobe; NE, norepinephrine; OFA, occipital face area; PMv, ventral premotor area; pSTS, posterior superior temporal sulcus; PTSD, post-traumatic stress disorder; RT, reaction time; STS, superior temporal sulcus; TEC, trauma exposed control; TMS, transcranial magnetic stimulation; TPJ, temporo-parietal junction; UCS, unconditioned stimulus; VAS, ventral affective system; vmPFC, ventromedial prefrontal cortex; vlPFC, ventrolateral prefrontal cortex; WM, working memory

* Corresponding authors at: Beckman Institute for Advanced Science & Technology, University of Illinois at Urbana-Champaign, 405 North Mathews Avenue, Urbana, IL 61801, USA.

E-mail addresses: fdolcos@illinois.edu (F. Dolcos), sdolcos@illinois.edu (S. Dolcos).

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1. Introduction and basic notions

Decades of research have shown that emotional stimuli can benefit from enhanced perceptual processing due to their ability to capture attention, and through such prioritized processing they also impact other cognitive processes. For instance, emotional stimuli are better encoded and remembered and can also be powerful distracters when task-irrelevant. Moreover, altered processing of emotional material has been associated with individual differences in various domains of healthy functioning (sex, personality, age), as well as with symptoms of affective disturbances, including anxiety and depression. The linguistic search that builds the foundation of this special issue reflects the centrality of attentional processes in affective experiences. The identified terms (Supplementary Table 1) can be broadly categorized into domains relating to conscious awareness, motivational effects of attention, social attention, and emotion regulation. We integrate the discussion of these terms within a broader review of emerging scientific evidence regarding emotion-attention interactions. We review evidence in healthy functioning and alterations observed in clinical conditions, with a particular emphasis on the associated neural mechanisms. This work brings together evidence based on various approaches, spanning from behavioral and lesion to brain imaging and interventions, which are grouped around the following four main themes: (1) *Emotion-Attention Interactions in Perception*, (2) *Emotion-Attention Interactions in Learning and Memory*, (3) *Individual Differences in Emotion-Attention Interactions*, and (4) *Training and Interventions to Optimize Emotion-Attention Interactions* (Fig. 1). A detailed discussion of evidence regarding these four themes is followed by a brief discussion of related linguistic aspects (5). Such a comprehensive approach allows for an integrative understanding of the available evidence and identification of concrete avenues for future investigations. In the remainder of this introductory section, we briefly introduce basic concepts that are relevant throughout the review.

1.1. Emotions vs. feelings

The nature of emotions has been a matter of centuries-long debate (e.g., Adolphs, 2016; Adolphs and Andler, 2018; Barrett, 2006, 2012, 2017; Ekman, 1999; Hamann, 2012; Kragel and LaBar, 2016; Panksepp, 2007). For instance, on the one hand, proponents of the “basic emotions” view argue that certain emotions (e.g., anger, fear, happiness, sadness, and disgust) are biologically basic, with each arising from a specific module in the brain with homology across species (e.g., Ekman, 1999; Tracy and Randles, 2011). On the other hand, proponents of the “constructionist¹” view posit that what the basic emotion theorists call ‘emotions’ are populations of instances (i.e., *categories*) that do not arise from their own dedicated neural modules, but instead are constructed from a combination of activity in domain-general networks of the brain that perform more basic psychological functions such as salience detection, memory, sensory perception, and language (Barrett, 2006, 2012; Barrett and Satpute, 2013). While definitions of *emotion* remain hotly debated (Lindquist et al., 2013; Panksepp, 2007), there is a

¹ Although this debate on the nature of emotion is not the focus of this manuscript, it is important to note that current theories of emotion have implications for the treatment of mental disorders in which emotion-attention interactions are maladaptive (see Section 4.3 below). For instance, a psychological constructionist approach has been applied as a way of understanding the mechanisms of PTSD, suggesting that core symptoms of this disorder might emerge from dysregulation of basic psychological operations or how these processes influence and constrain each other (Suvak and Barrett, 2011). Notably, this approach could be particularly useful in better understanding the heterogeneity of intrusive and re-experiencing symptoms experienced by PTSD patients (e.g., Dalgleish, 2004), which might be at least in part due to individual variations in the combination of dysfunctional psychological “ingredients” (Suvak and Barrett, 2011).

general consensus that *affective phenomena* (the more comprehensive term) consist of multiple subcomponents including physiological, appraisals, expressions, and behaviors that define the relation between the individual and environment. From a practical standpoint, a simplistic dissociation between *emotions* and *feelings* that is typically used in neuroscientific approaches is in terms of physiological vs. psychological aspects of affective processing (Iversen et al., 2000; LeDoux and Brown, 2017). Namely, while emotions have more to do with bodily responses (e.g., increased heart rate in a frightening situation), feelings refer to the associated psychological aspects (e.g., experiencing the feeling of being afraid) produced by the specific circumstances. Feelings might therefore be best understood as subjective interpretations of physiological responses (Siddharthan et al., 2018). Studies of emotion-attention interactions have investigated both emotions (including unconscious/automatic bodily responses) and feelings (relatively more conscious aspects of emotional responses), which are discussed throughout all sections of the current review.

1.2. Transient vs. long-term responses

In addition to differentiating between emotions and feelings, it is also important to consider the duration of affective experiences. What is commonly referred to as an occurrence of an emotion is transient and usually concerned with a specific object or situation (Russell and Barrett, 1999), whereas *mood* is considered to be much longer-lasting, diffuse, and less specific (Frijda, 2009). Furthermore, although emotions tend to follow the emotion-eliciting stimuli closely or instantaneously, a mood might be temporally remote from its cause, making the cause of a mood difficult to identify (Morris, 1992). Moreover, prolonged emotional responses and moods are also commonly observed as symptoms of anxiety, depression, or trauma- and stress-related disorders, which are characterized by recurrent and intrusive thoughts about previous or anticipated distressing or potentially traumatic events (Dalgleish and Power, 2004). Of particular relevance for the present review, such symptoms of affective dysregulation have been associated with deficits in top-down attentional control (Schäfer et al., 2018). These and other relevant issues are discussed in more detail in several sections of the present review.

1.3. Valence vs. arousal

These two basic affective dimensions, one referring to the (un)pleasantness and the other to the intensity of emotional responses, are commonly used to characterize various forms of affect (Lang et al., 1993; Russell and Barrett, 1999). Although different models proposed over time have emphasized either one or the other (Thayer, 1989; Watson and Tellegen, 1985) of these two dimensions, most current approaches agree with a bi-dimensional structure, with valence varying from positive to negative and arousal from high to low (Lang et al., 1993; Russell and Barrett, 1999). In the context of experimental manipulations, valence and arousal may be more difficult to separate because stimuli used to induce positive and negative emotions typically also determine a change in arousal (Lindquist et al., 2016). Hence, it is not only important to examine the role of positive and negative stimuli in attention and the associated processes, but also to dissociate between different levels of arousal within the emotional categories, which can be attained (Shafer et al., 2011).

1.4. Affect vs. motivation

Affective and motivational processes are closely related to one another (Lang and Bradley, 2008; Rolls, 2000), but the two have been conceptualized as being distinguishable and also different in terms of their effects on our cognition and behavior (Chiew and Braver, 2011; Pessoa, 2013). For instance, unlike affective processes, motivation is more explicitly goal-oriented and is thought to be the driving force for

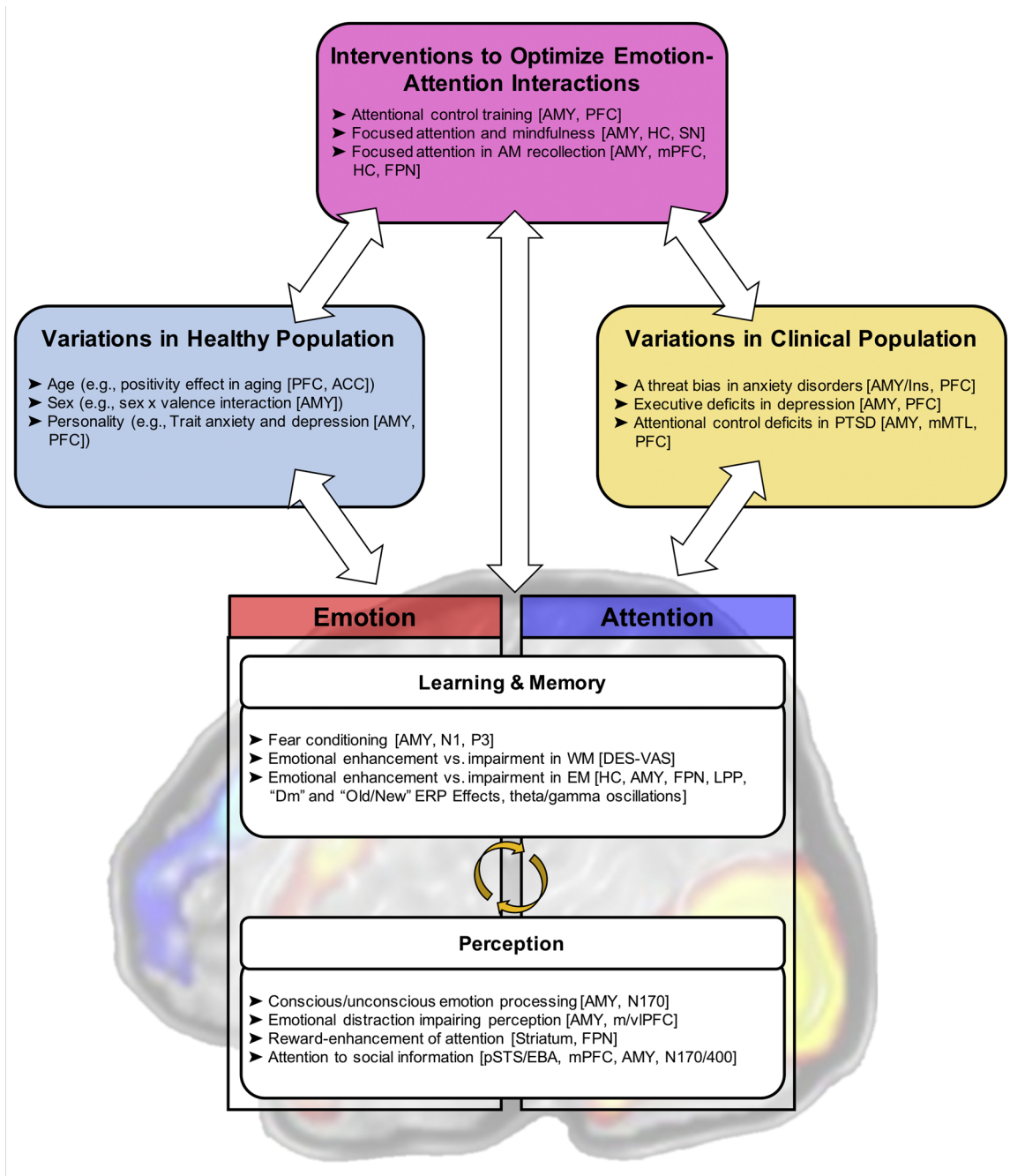


Fig. 1. Diagram of emotion-attention interactions discussed in the present manuscript. The figure summarizes domains and levels of emotion-attention interactions, along with associated neural correlates, based on behavioral, lesion, brain imaging, and intervention studies in healthy and clinical populations. Brain regions and event-related potentials (ERP) components within the square brackets denote the representative effects for each subsection featured in the manuscript. The color-coded brain activations in the background depict responses in a dorsal executive neural system (DES) involved in “cold” cognitive/executive processing and a ventral affective system (VAS) involved in “hot” emotion processing (brain image adapted from Dolcos and McCarthy, 2006). This image is used to suggest that emotion-attention interactions in the brain occur in the context of interactions between neural systems involved in executive and affective processing. AMY, amygdala; PFC, prefrontal cortex; ACC, anterior cingulate cortex; HC, hippocampus; mMTL, memory-related medial temporal lobe regions; mPFC, medial prefrontal cortex; vlPFC, ventrolateral prefrontal cortex; Ins, insula; pSTS, posterior superior temporal sulcus; EBA, extrastriate body area; DES, dorsal executive system; VAS, ventral affective system; FPN, fronto-parietal network; SN, salience network; LPP, late positive potential; WM, working memory; EM, episodic memory; PTSD, post-traumatic stress disorder.

actions engaged to accomplish the goals (Pessoa, 2009). In this context, affective experiences reflect the extent to which the goals are accomplished or not (and the associated rewards or punishments are obtained or avoided, respectively), and can also be experienced in earlier stages - e.g., during the planning of actions, or in the anticipation of accomplishing or failing to accomplish the goals. Similar to the valence dimension in affective processes, distinctions are also made between

approach and avoidance motivations, both at the level of temperamental tendencies (Gray, 1970; Higgins, 1998) and experimentally induced transient motivational orientations, which differentially modulate attentional flexibility (Calcott and Berkman, 2014; Gable and Harmon-Jones, 2008). In the present review, the role of motivation is discussed with respect to the impact of reward on attentional processes, as well as in the context of emotion-attention interactions in social cognition. It is

important, however, to also consider the different ways in which dispositional or momentary motivational states (Higgins, 1998; Higgins et al., 2012; Mischel and Shoda, 1995) can drive affect, attention, and their interaction (Dweck et al., 2004; Pessoa, 2014; Raymond, 2009).

1.5. Attentional processes

Finally, it is important to acknowledge that researchers have investigated different types of attentional processes and their interactions with emotion, although the focus of this review is not to distinguish between these different types at every level. For instance, a prominent view in the literature points to the existence of two anatomically and functionally distinct attentional systems in the brain, subserving top-down/goal-driven allocation of attention vs. bottom-up/stimulus-driven attentional processing (Corbetta and Shulman, 2002), both modulated by emotional information. A notable point highlighted by the research of these two attentional systems, for example, is that the interaction between emotion and attention is complex and intertwined, can go in either direction, and can involve both top-down and bottom-up processes. Furthermore, researchers have also differentiated between “selective” attention, characterized by differential processing of simultaneous sources of information (Johnston and Dark, 1986) and “sustained” attention, characterized by one’s readiness to detect certain signals over prolonged periods of time (Sarter et al., 2001). Yet, another line of research has investigated executive control of attention, or “executive” attention, defined as detection and resolution of conflict (Posner et al., 2007). Emotion-attention interactions linked to the various aspects of attentional processes are discussed throughout all sections of the current review, from links to early stages of perceptual processing and the impact on working memory, to their long-term influences on learning and memory, and linked to the role of individual differences in healthy and clinical groups, as well as in the context of training and intervention approaches targeting optimal emotion-attention interactions.

2. Emotion-attention interactions in perception

2.1. Conscious and unconscious emotion processing

Over the last two decades, research in the field of emotion processing has seen a rapid rise in interest, particularly with the increased availability of brain imaging methodologies. Furthermore, with the emergence of behavioral evidence showing that emotional stimuli can impinge on behavior after very brief presentations (tens of milliseconds), interest has also arisen in identifying and understanding unconscious processing of emotional stimuli, thus challenging the dominant idea upheld until then that affect could not occur without conscious cognitive processing (Zajonc, 1980). Subsequently, using behavioral measures, as well as brain imaging methodologies in both healthy controls and brain-damaged patients, a number of investigations have been carried out to determine the extent of these effects, as well as their neural substrates. These will be briefly overviewed below according to the experimental approach used, with a focus on the processing of emotional expressions.

2.1.1. Behavioral evidence

Numerous behavioral methods are available to disrupt awareness of the emotional stimuli in healthy participants. Among them, the most common involve (i) pattern masking procedures, in which the stimulus is presented very briefly and followed by (or also preceded by) a mask, and (ii) continuous flash suppression, in which different inputs (one flashing and one stable) are presented to each eye, consequently interfering with awareness of the stable stimulus (reviewed in Axelrod et al., 2015). In two original studies, Öhman and colleagues (Esteves et al., 1994; Öhman et al., 1989) demonstrated that conditioned angry faces produced an electrodermal response even when they were

masked, an observation that was later replicated with conditioned images of spiders and snakes (Öhman and Soares, 1993). Elsewhere, it was found that subliminally presented angry and happy faces primed the pleasantness ratings of Chinese ideograms (Murphy and Zajonc, 1993), as well as emotional memory (Yang et al., 2011) and produced shifts in spatial attention towards the threatening faces (Mogg and Bradley, 1999). Although masking thresholds appear to differ between individuals (Pessoa et al., 2005), evidence of emotional expressions has also been found with other techniques including sandwich masking (Stein et al., 2014).

2.1.2. Lesion evidence

Focal brain lesions provide a different source of evidence for emotion processing outside of conscious awareness. Some of the most compelling demonstrations stem from work by de Gelder et al. (1999), who were the first to report that blindsight (residual visual processing in patients with blindness due to damage to the visual cortex) extended to emotional expressions. Investigating a patient with right hemianopia (blindness in the right visual field), the authors found that when emotionally expressive faces were presented to his blind field, he performed above chance when guessing what the expression was. This affective form of blindsight revealed that the emotional information present on a face could be processed despite cortical blindness and thus in the absence of any conscious visual experience. Further evidence of affective blindsight was later found in another patient with bilateral visual cortex damage and complete blindness, who also demonstrated above-chance performance when guessing the emotional expressions on faces (Pegna et al., 2005). Functional magnetic resonance imaging (fMRI) recordings of this individual revealed the presence of right amygdala (AMY) activation when viewing faces with different emotional expressions.

Interestingly, affective blindsight is not restricted to facial expressions, but is also observed for emotional body expressions (de Gelder and Hadjikhani, 2006). Another patient, also suffering from bilateral cortical blindness, demonstrated the acoustic startle response to a conditioned visual stimulus that had been paired with an unpleasant electric shock (Hamm et al., 2003). Similar effects were observed in a separate fMRI study performed on a hemianopic patient, who showed AMY activity in response to unseen fearful faces and fear-conditioned stimuli (Morris et al., 2001). A particularly important point to highlight is that, in this hemianopic patient, activity in the superior colliculus and pulvinar was correlated to that in the right AMY, as has also been observed in healthy controls (see below). This suggests that affective blindsight could rely on a colliculo-pulvinar pathway to the AMY, as a neural substrate for unconscious processing of emotional stimuli. Finally, other approaches have corroborated the existence of unconscious processing of emotional faces and bodies, in particular using measures such as saccadic eye-movements towards unseen stimuli in the blind field (Bannerman et al., 2010), interhemispheric summation (Bertini et al., 2013), or physiological motor responses including pupil dilation and facial reactions, thought to reflect the emotional response to the unseen, yet processed stimuli (Tamietto et al., 2009).

Finally, evidence consistent with this idea also comes from research on patients with lesions in other brain regions, such as the parietal cortex. Lesions of the parietal lobe are known to produce attentional deficits, such as unilateral spatial neglect, while the primary visual regions continue to process basic information (Rees et al., 2000). Here, too, despite the inability of patients to report stimuli in the neglected or extinguished field, numerous findings have demonstrated that a certain degree of unconscious processing of emotional information does occur (Vuilleumier and Schwartz, 2001). Namely, patients generally do not report the stimuli presented in the contralesional (left) field, except when they were composed of emotional faces (see also Pegna et al., 2008a). These findings suggest that emotional stimuli (typically faces) have an overriding effect on the attentional deficit, thus indicating a certain degree of pre-attentive processing. As also discussed in the next

section, structures underlying this unconscious emotional face processing have been further explored using a similar task while brain imaging data were recorded (Vuilleumier et al., 2002), and point to the role of both subcortical and cortical brain areas in pre-attentive emotion processing.

2.1.3. Brain imaging evidence

Further evidence for unconscious emotion processing has come from research capitalizing on brain imaging approaches such as fMRI and electroencephalography (EEG)/event-related potentials (ERP) investigations (see Tamietto and de Gelder, 2010 for a review). Consistent with evidence from lesion studies, early fMRI research helped to localize brain regions that are important for emotion processing by capitalizing on the high spatial resolution of the technique. Research in this area established the AMY as a critical component for emotional face processing in humans, particularly for fearful expressions (Adolphs et al., 1994; Whalen et al., 2001). Presenting masked fearful and happy faces, Whalen et al. (1998) observed increases in AMY activity for fearful compared to happy faces. Interestingly, in a subsequent study (Whalen et al., 2004), the authors observed that the masked whites of the eye were sufficient to produce the AMY response. Using an aversive learning procedure, Morris et al. (1998) also found evidence of AMY activation for unseen, negative stimuli that were paired with an aversive noise. Subsequent analyses revealed increased connectivity between the right AMY and pulvinar and superior colliculus, for non-seen fear-conditioned faces, again substantiating the notion that a colliculo-pulvinar pathway to the AMY likely mediates emotion processing in the absence of awareness (Morris et al., 1999). AMY activation for non-conscious emotional processing has since been repeatedly confirmed using subliminal masking (e.g., Liddell et al., 2005), as well as binocular rivalry (Williams et al., 2004), confirming its ability to process emotions in the absence of awareness.

Evidence from EEG/ERP studies provided further insight into the timing of these phenomena, by capitalizing on the high temporal resolution of the technique to examine the brain responses to subliminal emotional faces. Although EEG/ERP has relatively low spatial resolution compared to fMRI, it allows for highly accurate characterization of the time course involved in high-level cognitive functioning, within the first second after the stimulus onset (Wilding and Ranganath, 2011). This technique has been shown to be a highly suitable tool to study the temporal dynamics involved in emotion-cognition interactions (Luck, 2005), whereas fMRI is well suited for studying spatial dynamics of the brain but has relatively low temporal resolution, making the two techniques complementary in this respect (Moore et al., 2019). In the ERP domain, increased N170 responses are associated with face processing (Allison et al., 1999; Stekelenburg and de Gelder, 2004). The N170 refers to a negative deflection in the occipito-temporal sensors of the ERP signal occurring around 130–200 ms post-stimulus onset, and is one of the most studied ERP components² in social, affective, and cognitive neurosciences to date (Botzel and Grusser, 1989; Eimer, 2011). Facial emotional expressions are processed in early ERP components, between 100 and 200 ms (in particular the N170) for fearful faces (e.g., Stekelenburg and de Gelder, 2004), as well as for other emotional expressions (Batty and Taylor, 2003; Hendriks et al., 2007). Furthermore, similar time periods were reported for the processing of

emotional body expressions (Stekelenburg and de Gelder, 2004), as well as naked bodies (Hietanen and Nummenmaa, 2011) and their perceived attractiveness (Del Zotto and Pegna, 2017) (see also Section 2.4 for a discussion of N170 related to face and body perception). In parallel with these observations, studies examining the time course of masked, subliminal, emotional faces reported differences between fearful and neutral faces in the 140–180 ms time windows (Pegna et al., 2011; Pegna et al., 2008b). Together, these findings highlight the N170 as an example of brain responses that appear to be sensitive to emotional, social, and cognitive processing, including during masking, which makes it a useful target for investigating multiple aspects of emotion-attention interactions.

Unconscious emotion processing has been proposed to be an artefact of incomplete masking (Pessoa et al., 2005), and thus it was again argued that fearful faces may not actually be processed automatically and non-consciously, and that previous results may be explained by the fact that awareness was not sufficiently controlled (Pessoa et al., 2006). Counterarguments to this idea have risen when considering situations where either awareness was impeded by orienting attention away from the emotional stimuli, thus precluding detection, or the emotional stimulation was not powerful enough (Vuilleumier et al., 2001). Moreover, as described below, results from a more recent investigation (Shafer et al., 2012) provide evidence reconciling the opposing views (see work by Vuilleumier et al. vs. Pessoa et al.) regarding the debate about the automaticity of emotion processing, by demonstrating that processing of emotional information is both automatic and modulated by attention (Shafer et al., 2012).

Overall, although some degree of controversy remains, the available behavioral, lesion, and functional neuroimaging evidence strongly supports the view that the processing of emotional information in humans can occur without awareness. The entire network involved in these processes may not yet have been completely identified, but it appears that the AMY plays an important part in its implementation. Despite evidence suggesting an early time course for the processing of emotional stimuli under conditions of conscious and unconscious viewing, the link between these early differences and AMY activation remain to be determined. Another element that remains unclear is the diversity of emotional stimuli that might be processed without awareness. Although faces have been used in a large majority of investigations, other stimuli, such as body expressions, have recently begun to be studied (see de Gelder et al., 2010 for a review on this topic), and other types of emotional stimuli may likely also be processed unconsciously. For example, there has been a growing body of work on the link between motivation and attention in the context of conscious and unconscious processing of reward (Bourgeois et al., 2016). However, an additional challenge for this research area is that the paradigms used tend to have stimuli that predict reward and have an inherent value of motivational significance in the task itself. Section 2.3 provides more details on the links between reward and attentional processes. One last crucial point of discussion concerns the pathways leading to AMY activation, in the context of unconscious processing. As alluded to above, one influential hypothesis has suggested that unconscious processing of emotional stimuli may arise through a subcortical pathway to the AMY, which involves the superior colliculus and the pulvinar (LeDoux, 2012). Although evidence is emerging supporting the existence of this pathway both functionally (e.g., Garrido et al., 2012) and anatomically (Tamietto et al., 2012), its existence remains highly debated (de Gelder et al., 2011; Pessoa and Adolphs, 2010) and is yet to be resolved.

The wealth of evidence accumulated to date confirms the validity of nonconscious processing, and arguably, most emotional and cognitive processes generally occur outside of awareness. What remains unclear is whether unconscious processes reflect weak(er) but comparable modes of brain function to conscious ones, or whether the two modes of processing are distinct, which is a question akin to whether consciousness is a graded or an all-or-none phenomenon (e.g., Overgaard and Mogensen, 2014; Sergent and Dehaene, 2004). While still an open

² Here, and in Section 2.4 below, we focus our discussion on N170 responses in the context of examining conscious and unconscious processing of social-affective stimuli (i.e., faces and bodies). It is important to note, however, that available evidence demonstrates that N170 can also be modulated by other factors, such as expectations. For instance, greater N170 responses have been associated with processing of deviant faces, suggesting that this ERP component reflects at least in part a prediction error signal in social perception (Johnston et al., 2016). Given its sensitivity to both bottom-up stimulus features and top-down goal relevance, the N170 seems to play broad roles in social, affective, and cognitive processes associated with emotion-attention interactions.

question, the fact that evidence appears to favor the latter (e.g., Dehaene and Changeux, 2011; Williams et al., 2006) strongly justifies maintaining this area as an independent field of investigation.

2.2. Emotional distraction and perception

2.2.1. Emotion-attention interactions in the impact of distraction on perception

An important factor in determining the impact of emotion on perception and attention is whether emotional stimuli serve as targets (task-relevant) or distracters (task-irrelevant). When an emotional stimulus is task-relevant, the prioritization of processing resources for affective information results in task-enhancement, whereas when it is task-irrelevant, emotion processing can lead to depletion of resource availability and result in task-impairment (Dolcos et al., 2011; Iordan et al., 2013b). This was also the case in the studies discussed above leading to opposing views regarding the automaticity of emotional processing vs. its dependence on the availability of processing resources. A recent investigation provided reconciling evidence regarding the automaticity of emotion processing (Shafer et al., 2012), by manipulating both aspects of controversy identified by previous research. Specifically, this study investigated the impact of emotional distraction on performance in a shape discrimination task, by manipulating both (i) the degree of emotional charge of the distracting information (from highly to absolute neutral) and (ii) the attentional demands of the main cognitive task, by varying the task difficulty (low vs. high perceptual load) and the time of presentation (short vs. long duration). Behavioral findings revealed impaired performance by emotional distraction reflected in longer reaction times (RTs) for negative than for neutral items, regardless of manipulations of attentional demands. However, the detrimental effect of emotional distraction was strongest when the difference in emotional content was the greatest (highly emotional vs. absolute neutral comparison) and the attentional resources were most available (low load).

These findings are consistent with the idea that processing of emotional information can be both automatic (when emotional stimuli are powerful) and susceptible to attentional modulation (when processing resources are low). Paralleling these behavioral effects, and consistent with the traditional view regarding the automaticity of emotion processing (Vuilleumier, 2005), activity in basic emotion-related regions (e.g., AMY) was found in response to emotional stimuli, regardless of manipulations of attentional demands. However, the engagement of higher-level (cortical) emotion processing regions (i.e., medial prefrontal cortex [mPFC] and ventrolateral PFC [vlPFC]) showed susceptibility to modulation by attention, with increased engagement when attentional resources were most available and there was more time to perform the task (Shafer and Dolcos, 2012). Hence, depending on the circumstances, emotional information can be processed automatically and is also susceptible to modulations linked to the availability of attentional resources. Overall, these findings provided reconciling evidence regarding the automaticity of emotion processing, which has been the focus of a long-lasting debate in the literature (Pessoa, 2013; Vuilleumier, 2005).

2.2.2. Emotion-attention interactions linking the impact of distraction on perception and episodic memory

Attention-perception interactions affect not only initial perception but can also have long-term consequences on memory (see also the section on learning and memory). Specifically, emerging evidence suggests that emotional distraction has opposing immediate vs. long-term effects, which are influenced by attentional modulation. Such evidence provides neural support for opposing effects of emotion in real-life situations, where task-irrelevant emotional information (e.g., the scene of a tragic accident while driving) may temporarily distract us from the main task (e.g., driving), while also leading to better memory for the distracting information (e.g., the crashed vehicles). Task-

irrelevant emotional distracters can impair ongoing cognitive processing (e.g., perceptual), while also leading to enhancement of memory for the distracters themselves (Shafer and Dolcos, 2012). Importantly, this study provides evidence that immediate/impairing and long-term/enhancing effects of emotional distraction are differentially influenced by the availability of processing resources. Specifically, while the strongest immediate impairment of emotional distraction occurred when processing load was low, and thus there were more processing resources available, the strongest enhancement of episodic memory for the emotional distracters occurred when processing resources were least available (high load).

At the neural level, the dissociation between these two opposing effects was observed in both basic AMY-hippocampus (HC) mechanisms and in higher-order cognitive brain regions (mPFC and parietal cortex). Specifically, the results point to a possible hemispheric dissociation identified in the AMY–HC mechanisms, with bilateral engagement for the impairing effect and left-sided engagement for the memory enhancement by emotion. This finding can be linked to evidence suggesting greater engagement of the left AMY in more elaborative processing of the emotional stimuli, which also contributes to enhanced memory (Glascher and Adolphs, 2003; Phelps et al., 2001). Outside of the MTL, the mPFC was associated only with the immediate/impairing effect on perception, whereas the superior parietal cortex was associated only with the long-term/enhancing effect on memory. Given that mPFC is sensitive to emotional stimuli (Keightley et al., 2003) and the superior parietal cortex is part of the dorsal attentional network (Corbetta and Shulman, 2002), the contribution of these regions to the opposing effects can be attributed to increased emotional and attentional processing of the distracters, respectively (Shafer and Dolcos, 2012).

2.3. The role of reward in attentional processes

The vast majority of evidence regarding emotion-attention interactions capitalizes on the impact of negative emotional responses, produced by stimuli with powerful motivational significance. However, positive motivation is also an effective way to induce and sustain goals, and thus promote goal-directed attention – e.g., when participants are told that they will receive reward for correct performance or when a stimulus predicts future rewards (Braver, 2016). Similar to negative emotional information, stimuli associated with reward or signaling potential future reward (or loss of reward) can also contribute to distraction, if such signals are incongruent with the task at hand (Anderson et al., 2013). Here, we discuss the influence of reward on attentional processes, underlying neural substrates, and associations with behavior.

A growing number of studies have shown that incentives or positive reinforcement (i.e., gaining monetary or other forms of reward for correct performance) improve accuracy (Gilbert and Fiez, 2004) and performance in cognitive tasks (Krawczyk et al., 2007). Such improvements are thought to be associated with the effects of reward on the deployment of attentional resources. Some researchers have argued that reward influences attention by improving the quality of sensory coding, as it mobilizes attentional resources in ways that can promote access to better representation of the information (Hübner and Schlösser, 2010). According to the dual mechanisms of control framework (Braver, 2012), the use of incentives is thought to improve task performance by increasing *proactive* control (i.e., preparatory control aimed at preventing conflict and optimizing task performance) through sustained activation of task-relevant information. For instance, Chiew and Braver (2016) reported that task-informative cues in the flanker task, signaling whether an upcoming trial was incongruent, could reduce interference, but only when cues were paired with rewards and there was sufficient preparation time (Chiew and Braver, 2016). However, there is also evidence that reward can increase *reactive* control (i.e., rapid adjustment of control in response to performance monitoring), such as speeding up response inhibition in a stop-signal task

that does not include preparatory cues (Boehler et al., 2014).

Studies focused on attentional control or conflict processing report reduced conflict during the reward versus no-reward condition as indexed by more accurate and faster reaction times (Padmala and Pessoa, 2011). Specifically, Padmala and Pessoa reported reward cue-related responses in subcortical regions (including striatal - nucleus accumbens, caudate, putamen - and ventral tegmental area) and fronto-parietal attentional regions. Interestingly, they showed that activation in these fronto-parietal regions was predictive of reduced conflict-related signals in the mPFC during the target phase of the task. They also reported findings from path analyses suggesting that a relationship between the right intraparietal sulcus (IPS) (during reward cue) and the mPFC (during target) was mediated by neural responses in the left fusiform gyrus (FG) (during target). Such findings support the notion that reward can 'upregulate' attentional control and that such upregulation depends on how reward-related subcortical regions interact with fronto-parietal regions important for the control of attention (Padmala and Pessoa, 2011).

Reward could also impede performance on cognitive tasks by modulating early attentional processes in ways that would impair the ability to maintain task representations and reduce goal-directed attention necessary for optimal task performance (Anderson and Sali, 2016). Numerous recent studies have provided evidence that when visual features of a stimulus are associated with a reward outcome, they acquire high priority and can automatically capture visual attention (e.g., Anderson et al., 2013). Such attentional capture is also dependent upon the individual's learning history (Anderson, 2017). Learning which stimulus or object is more likely to predict a reward outcome of high value (e.g., money, food, positive social feedback from peers) creates reward-related attentional biases that can override goal-directed attention. As demonstrated by a series of experiments, the capture of attention by a neutral, task-irrelevant distracter, which had been previously associated with monetary reward, was associated with the slowing of RTs to a shape target (Anderson et al., 2011). ERP studies revealed that non-contingent reward cues modulate the amplitude of ERPs associated with cortical activity in early visual areas, indicating that such cues might alter the properties of perception (Hickey et al., 2010). Findings from neuroimaging studies suggest the involvement of 'value-driven attention network' implicated in reward-related attentional capture, which includes striatal regions, such as the caudate, as well as sub-regions of the visual cortex, and the IPS (Anderson and Sali, 2016).

Finally, the development of fronto-striatal networks is an important factor to consider regarding the influence of reward on attention. Such influences could be attributed to the age-related peak in reward and sensation-seeking behaviors (Steinberg et al., 2009), sensitivity to monetary incentives (Galvan et al., 2006), and other forms of reward (Eckstrand et al., 2017). Several neuroimaging studies report elevated activation of ventral striatum to anticipated reward or appetitive cues in adolescents compared to adults or children (Galvan, 2010; Geier et al., 2010). Other studies indicate that the neural systems involved in integrating motivationally salient information with attentional control processes, including ventrolateral fronto-striatal networks (Balleine et al., 2007; Delgado et al., 2004), remain less structurally and functionally mature during the adolescent years (Rubia et al., 2006; Somerville et al., 2010). Few studies have examined specifically, however, the influence of reward on attentional processes, and the findings are mixed, with some reporting that incentives facilitate adolescent cognitive control (Padmanabhan et al., 2011), and others reporting reduced effects compared to adults (Castel et al., 2011). Such findings suggest that neurodevelopmental changes in fronto-striatal systems may contribute to changes in how reward influences attentional processes.

In summary, numerous studies have shown that reward can enhance attention in selective ways and that such enhancement can promote goal-directed attention or capture selective attention in ways that can

impede performance. The neural correlates associated with these effects involve fronto-striatal interactions, and their developmental trajectory may influence the effect of reward on attentional processes.

2.4. Emotion-attention-perception interactions in social cognition

2.4.1. Face and body perception

The nature of our interactions with others depends critically on how we perceive and interpret their emotions, which can also provide insight into intentions and future actions. While these are typically expressed in both the face and the body, research on perception of emotions in both categories has run asynchronously, with face research preceding the scientific study of bodies by several decades. Both faces and bodies convey information about multiple variables including sex, age, identity, and emotion. As a category of stimuli with high behavioral relevance, processing of body forms has been studied with similar behavioral and neural methods to faces, and the findings on associated processing mechanisms turned out remarkably parallel to those of faces. For instance, both faces and bodies are processed configurally (Reed et al., 2003; Stekelenburg and de Gelder, 2004), which relates to the dominance of perception of spatial relations between features over the perception of the features themselves. This proposed mechanism is typically investigated by means of the inversion effect, which refers to the difference in recognition performance of stimuli presented upside-down compared to stimuli presented in a canonical orientation (upright). While an inversion effect is not face- or body-specific, it is increased for faces and bodies compared to other stimulus classes, such as houses or shoes (Reed et al., 2003; Stekelenburg and de Gelder, 2004).

At the neural level, both faces and bodies are associated with electrophysiological (ERP) and hemodynamic (fMRI) markers. As reviewed above in Section 2.1, in the ERP domain, increased N170 is typically associated with face processing (Allison et al., 1999; Stekelenburg and de Gelder, 2004), and is presumed to underlie structural encoding. Behavioral and EEG studies using a delayed match to sample task have found an inversion effect for bodies, with a longer RT for inverted bodies (Reed et al., 2003), and similarly delayed, but enhanced N170 ERP components for both inverted faces and bodies (de Gelder et al., 2010; Stekelenburg and de Gelder, 2004). The fMRI-based research has identified both body- and body parts-specific areas in the fusiform gyrus (FG), between face sensitive clusters, termed fusiform body area (FBA), and in the lateral occipital cortex, termed extra-striate body area (EBA) (Downing et al., 2001; Peelen and Downing, 2007). For EBA, there is evidence that its activity is modulated not only by passive perception of bodies, but also by participants' own unseen hand- and foot-pointing movements (Astafiev et al., 2004). In addition to the body-specific EBA and FBA, the posterior superior temporal sulcus (pSTS) is activated by both bodies and faces, and is also activated by body motion (Kontaris et al., 2009). Body-specific patches have also been reported in the STS in non-human primates, partially overlapping with face-selective patches (de Gelder and Partan, 2009). These patches had single-cell responses to local fragments of the bodies, which were frequently but not exclusively present with body stimuli (Popivanov et al., 2016).

In addition to the information related to visual forms and recognition, human bodies also convey a much wider range of daily-life actions than faces. The dorsal stream is more activated by observation of bodies than by observation of faces, including activation in the action observation network (e.g. ventral premotor [PMv], middle and anterior parietal sulcus). The functions of PMv and EBA in body perception have been studied using transcranial magnetic stimulation (TMS). Stimulating EBA selectively slows the RT for form discrimination, while stimulating PMv selectively slows the RT for action discrimination (Urgesi et al., 2007). Emotional information can be conveyed efficiently by bodies, either depicted with static images or with dynamic video clips, or even with static or dynamic point-light displays alone (de Gelder and Van den Stock, 2008; Van den Stock et al., 2015). The

processing of emotional body cues occurs fast in healthy participants. In a magnetoencephalography (MEG) study, fearful bodies could be differentiated from neutral ones as early as 80 ms in parietal areas (Meeren et al., 2016). Emotional bodies often provide contextual information for processing other modalities such as faces, voices, and scenes, and interfere with them, but perception of emotional bodies can also be influenced by these kinds of contextual information (e.g., Van den Stock and de Gelder, 2012; Van den Stock et al., 2014).

Notably, emotional bodies activate the AMY presumably in interaction with body-specific areas - i.e. EBA, FBA, and pSTS (e.g., Hadjikhani and de Gelder, 2003; Pichon et al., 2012), similar to emotional faces recruiting the AMY and face-specific areas. Interestingly, threatening scenes also activate the EBA (Sinke et al., 2012b). Emotional bodies recruit action processing areas including the premotor cortex and emotion-related areas including the temporo-parietal junction (TPJ), temporal pole, and orbitofrontal cortex (e.g., Kret et al., 2011; Pichon et al., 2012).

Finally, the roles of PMv, EBA and parietal regions (inferior parietal lobule [IPL], anterior IPS) in bodily emotion processing were also examined in TMS studies, focusing more on the body-specificity and action-related aspects. Under binocular rivalry presentations of faces or bodies together with houses, stimulating pSTS decreased the dominance of fearful faces versus houses, but enhanced the dominance for fearful bodies (Candidi et al., 2015). In a body posture discrimination task, stimulating pSTS enhanced the detection of posture changes in angry bodies but not in neutral bodies. However, stimulating EBA and PMv did not show such an effect dissociating between angry and neutral postures (Candidi et al., 2011). Stimulating IPL enhances the processing of fearful bodies compared to stimulating EBA (Engelen et al., 2015). These studies highlighted the importance of dorsal action-related areas in bodily emotion processing, in opposition to evidence of heads processed in ventral face-specific areas, as suggested by a study reporting fMRI-adaptation for whole- compared to headless-bodies in fusiform (FFA) and occipital (OFA) face areas, instead of in EBA and FBA (Brandman and Yovel, 2010).

2.4.2. Higher-order perception in social cognition

Aside from influencing initial perceptual processes and attention paid to social stimuli such as faces and bodies discussed above, emotion-attention interactions also influence higher-order social cognition processes, such as impressions, judgements, and decisions (Freeman and Ambady, 2011). For example, when interacting with unknown others for whom no relevant information is available, people often depend on a variety of factors, such as physical appearance, verbal behavior (Ames et al., 2011), as well as nonverbal behavior, or affective body language (de Gelder et al., 2010), as cues to form impressions. Subtle cues conveyed through body language or physical touch, such as a handshake or a gentle touch on the shoulder, can lead to positive effects on behavior, reflected in greater feelings of security when making risky financial decisions (Levav and Argo, 2010) or better evaluations and better tips (Stephen and Zweigenhaft, 1986). During typical social interactions, people engage in active social perception processes, such as attending to others' face and body language, to evaluate the social situation. The majority of studies investigating the neural correlates of social cognition have tended to focus on faces or static whole body stimuli (Van den Stock et al., 2014), but emerging research also highlights the importance of dynamic whole body stimuli (Dolcos S. et al., 2012; Katsumi and Dolcos, 2018). These studies indicate that the neural network underlying whole body perception partly overlaps with the face network (de Gelder et al., 2010), and involves the AMY, the FG, and the STS. Both faces and bodies are salient and familiar in daily life, conveying information about the internal states that is essential for social interactions, but only bodily expressions allow perception of the action and of its emotional significance (Sinke et al., 2012a), and hence prepare the perceiver for adaptive actions.

Recent studies using dynamic bodily expressions have investigated

the respective contribution of emotion processing and action-related brain areas. Studies clearly show that the AMY is sensitive to the emotional significance of body movements (de Gelder et al., 2012) and modulates the engagement of body-selective areas (Peelen and Downing, 2007). This modulatory role of the AMY is consistent with research showing its involvement in several component processes, such as stimulus appraisal, relevance detection, activation of neuroendocrine responses, as well as somatic motor expressions of emotion (Sander et al., 2005). Given its many connections to brain areas involved in behavioral output (Mosher et al., 2010), the AMY is involved in assessing the relevance of stimuli, signaling what is important in any particular situation, and then modulating the appropriate attentional, perceptual, autonomic, and cognitive/conceptual processes to deal with the challenges or opportunities that are present (Cunningham et al., 2010; Laine et al., 2009). The AMY is also sensitive to encoding social information that is consistent, relative to inconsistent, with subsequent positive or negative evaluations of another person (Schiller et al., 2009). Together, the evidence highlights the role of AMY in processes relevant for perception as well as higher-level cognition such as impression formation.

Despite a large amount of research on the neural systems involved in processing social cognition, relatively few studies have examined how these regions are recruited when viewing social interaction scenes (Centelles et al., 2011; Iacoboni et al., 2004). This is important because, when viewing complex scenes involving social interactions, observers spontaneously attempt to make sense of what is happening during the social interaction (Wagner et al., 2012), by also engaging regions involved in mentalizing (Iacoboni et al., 2004), such as the mPFC (Amodio and Frith, 2006). Notably, recent research has examined the neural basis of social cognition within a relevant social context (Dolcos S. et al., 2012; Katsumi and Dolcos, 2018). Consistent with the roles of the AMY, STS, and mPFC described above, findings from this line of research highlight enhanced response to approach compared to avoidance behaviors in these regions (Dolcos S. et al., 2012), and that greater sensitivity to approach than to avoidance behaviors in AMY and STS was linked to more positive evaluations of approach behaviors. This research enhances the similarity to what happens in everyday life, where people are typically involved in dynamic interactions with others in a defined social context that guides their interpretation of the mental and emotional states of the target (e.g., Aviezer et al., 2008) and ultimately the evaluation of others' attitudes and behaviors (see also Dolcos S. et al., 2012; Katsumi and Dolcos, 2018).

Similarly, recent and emerging work with EEG/ERPs has expanded the research on emotion-attention interactions and social cognition to examine the dynamics of these processes. For example, early ERP components such as P200/N200, which are associated with attentional deployment (Luck and Hillyard, 1994), have been linked to early perception and categorization of group membership (Ito and Bartholow, 2009). ERPs in slightly later time windows, such as the N400/450, have been associated with the observation of actions, reflecting the extent to which certain actions are expected vs. unexpected in a given (social) context (Amoruso et al., 2013), as well as sensitivity to human presence during social encounters (Katsumi et al., 2019a). ERPs in later time windows, including the late positive potential (LPP), have been associated with processing of social information such as biological motion (Katsumi et al., 2019a; Proverbio et al., 2009), as well as with emotion processing (Dolcos and Cabeza, 2002; Schupp et al., 2006).

Finally, a recent model proposes that there are dynamic interactions between bottom-up signals, such as facial, vocal, and bodily cues, and top-down factors, such as stereotypes and prior knowledge, that lead to unified perceptions and responses to others (Freeman and Ambady, 2011). The kinds of information processed in the model include cue level inputs (i.e., face, body, and voice cues), category level factors (i.e., gender, race, age, emotion), stereotypes level factors, and high level cognitive states (Freeman et al., 2012), highlighting the interactions that can occur between these factors. This and other similar models are

helpful in furthering understanding of the complex number of factors that influence social cognition/evaluation, and further support the idea that emotion-attention interactions modulate higher-level social processes. Importantly, these models might help shed light on the factors that contribute to conditions where social-emotional functioning is impaired, such as autism and social phobia (Gilboa-Schechtman et al., 1999; Mazefsky et al., 2012).

3. Emotion-attention interactions in learning and memory

This section discusses evidence regarding emotion-attention interactions linked to implicit and explicit types of memory, with a focus on conditioning and working and episodic memory, respectively.

3.1. Fear conditioning

Our understanding of the detection of threat, the organization of defensive behaviors, and activation of the defense circuitry in the brain is based on animal studies primarily using Pavlovian fear conditioning as an experimental paradigm. Defensive adaptations to acute or anticipated threat associated with fear conditioning are characterized by a close interplay of cognitive (including attention) and emotional processes, as described below. Psychobiological models of defensive behaviors suggest that defensive reactivity is dynamically organized along a continuum depending on the imminence or proximity of the threat, from pre- to post-encounter defense, followed by circa-strike defense (Threat-Imminence Model; Fanselow, 1994; Defense Cascade Model; Blanchard and Blanchard, 1990; Lang et al., 1997; Action-Action Tendency Model; Schauer and Elbert, 2010; adapted from Hamm et al., 2016). These stages are accompanied by changes in the emotional and attentional responses (e.g., from hypervigilance, to selective attention, and attentive motor “freezing”) (Hamm et al., 2016).

3.1.1. Dynamics of defensive response mobilization

There is ample evidence in non-human animals suggesting that defensive behaviors are organized along a dimension changing from one to another depending upon the perceived proximity of the threat (Blanchard and Blanchard, 1990; Fanselow, 1994). When the organism is in an environment or a context in which a threat has been encountered before (or, in the case of humans, that the individual has just been informed - e.g., by others or media - that a threat might occur but has not yet been detected), a class of adaptive defensive behaviors (*pre-encounter defense*; Fanselow, 1994) are engaged to pre-empt hostile and threatening encounters. Such defensive behaviors include inhibition of appetitive behaviors, threat-non-specific hypervigilance, and increased autonomic arousal. Humans, in addition, often report feelings of *anxiety*, *apprehension*, or *worry* if they encounter such uncertain, novel, and ambiguous environments and contexts in which potential threats might occur (see Davis et al., 2010). As soon as the threatening stimulus is detected but is still distant, a defensive response is activated (*post-encounter defense*) that is characterized by an increase in selective attention to the threatening cue (or the cue that is associated with threat), accompanied by heart rate deceleration (fear bradycardia; Campbell et al., 1997), potentiation of the startle reflex, gated through the central nucleus of the AMY (for a review, see Hamm, 2015), and attentive motor “freezing.” In humans, this defensive response pattern is often labelled as a feeling of *fear* and individuals frequently report specific fear triggers. If the reported fear also causes significant distress or impairment, which is out of proportion of the actual danger (according to the [cultural] context), such defensive responses are diagnosed as symptoms of a Specific Phobia further specified and categorized according to the fear triggers (e.g., animal phobia, height phobia).

Finally, with increasing imminence of the threat (*circa-strike defense*), defensive response mobilization changes into action, which – depending on the behavioral options at hand – can result in a fight/flight response (if possible) or, when this is not an option, in tonic

immobility. Humans often report feelings of *panic* during circa-strike defense. Initiation of such defensive actions (Kim et al., 2013) is accompanied by sympathoexcitatory responses, like tachycardia, hypertension and redistribution of the blood flow (Benarroch, 2012). This general discharge of the sympathetic nervous system also stimulates the adrenal medulla to secrete the catecholamines epinephrine and norepinephrine (NE) into the blood stream. Besides direct physiological effects, adrenergic system activity modulates cognitive processes, especially the formation and consolidation of emotional memories (McGaugh, 2004; Weymar et al., 2009), thus resulting in better memory of emotionally arousing events (e.g., traumatic events). Such dynamic organization of defensive behaviors has been repeatedly advocated by many researchers (for reviews see Adolphs, 2013; McNaughton, 2011).

3.1.2. Dynamic defensive response organization during human fear learning

By transferring these findings to human fear learning, one has to keep in mind that human fear conditioning studies differ from animal studies in many ways. Human participants know in which kind of experiment they are participating and they have a free choice to do so or not. Moreover, human participants are typically asked to determine the level of aversiveness of the unconditioned stimulus (UCS) by themselves and they are informed that they can terminate the experiment whenever they want. Given these constraints, it is even more important to make sure that the measures of fear and anxiety are highly comparable with those obtained from animal research and not only include a single dependent variable (like skin conductance responses that are not specific indicators of fear but are also related to increased orienting) to assess fear learning in humans. As outlined above we can assume that human defensive behavior is also – like in non-human animals – dynamically organized. Thus, it is crucial to realize a multi-level analysis approach including behavioral, physiological, and neural indices of cognitive and emotional processes involved in the detection of threatening cues and contexts, as well as in the dynamic organization of defensive response mobilization. If this is taken into account, the organization of human defensive behavior is remarkably similar to that of animals as outlined in the theoretical model above.

As soon as the occurrence of the threat is predicted by a conditioned stimulus (distant threat) humans show a defensive response that is again highly comparable to the response pattern observed in animals. Humans – like rodents – show a reliable potentiation of the startle response, which is measured by recording electromyographic activity of the orbital portion of the orbicularis oculi muscle. This is elicited by acoustic probes (a 50 ms burst of white noise presented with instantaneous rise time) delivered during the conditioned cue previously associated with a shock, relative to the startle response to probes delivered during safety cues or during the intertrial interval (Hamm et al., 1993). Conditioned startle potentiation is substantially stronger if the conditioned cue predicts an aversive UCS, both in a single cue (Lipp et al., 1994) and in a differential conditioning (Hamm and Vaitl, 1996). Startle potentiation increases significantly with increasing temporal proximity of the UCS if there is not behavioral option to avoid the electrical stimulation (Löw et al., 2015).

Consistent with the role of AMY in these effects found in animal research (see Davis, 2000 for neural circuitry underlying fear-induced startle potentiation in rodents), fear conditioned startle potentiation is significantly impaired in patients with unilateral lesions of the AMY (Weike et al., 2005), while skin conductance conditioning remains intact. Supporting these findings, fear potentiated startle was completely blocked in a group of four female subjects with Urbach-Wiethe disease, despite learned contingency reported by half of these subjects (Klumpers et al., 2015). These data show that autonomic changes as well as verbal reports observed during aversive conditioning can be dissociated from fear potentiated startle and therefore reflect a different component of the learned fear response. While conditioned stimuli (CS) associated with an aversive UCS reliably elicit increase skin conductance response, such increases are elicited by almost any novel,

unexpected, arousing, significant, or potentially important stimulus in the environment, even by the omission of an expected stimulus (Siddle, 1991). Thus, rather than a specific indicator of defensive response activation, skin conductance responses have been interpreted as indexing increased orienting or selective attention to the reinforced CS. Accordingly, increased conditioned skin conductance learning has been observed not only for aversive but also for appetitive conditioning (Nitschke et al., 2002; Weike et al., 2008).

The entire pattern of defensive response adaptation that can be observed during Pavlovian fear conditioning where there is no option to escape from the unconditioned stimulus can be described as *attentive freezing*, which is comparable to the behavioral pattern observed in animals during post-encounter defense. The defensive behavioral pattern changes substantially, however, if humans have the behavioral option to actively avoid the unconditioned stimulus. Under these circumstances, humans show a sharp increase in skin conductance and a heart rate acceleration just prior to the initiation of the motor response. In this context of active avoidance, the startle response is no longer potentiated but rather inhibited. Moreover, the P3 amplitude of the ERP evoked by the startle probes during this active defense mode are also strongly inhibited while the N1 component of the same potential increases (Krause et al., 2017; Löw et al., 2015). These data also support findings in animals, suggesting that during circa-strike defense – where active defensive behavior is initiated – attention to irrelevant stimuli of the environment are selectively blocked while the sensory gain to the same stimulus seems to be increased.

3.2. Working memory

3.2.1. Affective working memory

Working memory³ (WM) is the capacity-limited resource that temporally maintains and stores information (Baddeley, 2003) in the service of higher cognitive functions (fluid intelligence, for instance; Kane et al., 2005). In everyday life, these cognitive functions are commonly deployed in affective contexts. Despite this, the impact of affective information on working memory and the mechanisms through which that impact is realized remain poorly understood (Schweizer and Dalgleish, 2016; Schweizer et al., 2019). However, the past two decades have seen an exponential increase in the research investigating the effects of affective information on WM performance. The impact of affective distracters on WM is discussed in the following section, and thus here we focus on affective WM, defined as WM for affective material.

3.2.1.1. Affective enhancement vs. impairment. The evidence regarding emotion-attention information reviewed in the sections above suggests that, as with perception, WM performance may also be enhanced or impaired by affective information depending on whether the affective material is presented as task-relevant memoranda or as task-irrelevant distracters⁴. Robust evidence from the long-term memory literature (reviewed below) shows an emotional enhancement effect (LaBar and Cabeza, 2006). This is proposed to be associated with enhanced early

encoding of the affective memory trace, which is then consolidated over time (Murty et al., 2010). Improved encoding is associated with increased recruitment of the AMY-HC complex in response to affective compared to neutral memoranda (Phelps, 2004). The mediation model of emotional memory (Talmi, 2013) argues that the mnemonic enhancement arises from three interacting processes, which can also be applied to affective WM. First, affective WM may be enhanced due to prioritizing of affective information within the context of limited attentional resources (Pourtois et al., 2013). Second, encoding of affective information is prioritized because affective relative to neutral information stands out (cf. the notion of "impact"; Ewbank et al., 2009). Third, encoding of affective information may be facilitated by the organization of the material into shared thematic links. Alternatively, however, WM for affective material may be reduced compared to neutral material, because the regulatory demands elicited by affective information draw resources away from WM processing. This argument is supported by the neural architecture underlying affect regulation and WM, as both processes depend on the recruitment of shared neural substrates in the fronto-parietal control network (Etkin et al., 2015). Here, we briefly review behavioral and neural evidence to resolve these competing hypotheses.

3.2.1.2. Behavioral effects. WM paradigms commonly require individuals to update information, such as numbers, letters, or shapes in their memory store, while simultaneously trying to minimize interference from other irrelevant material (e.g., Conway et al., 2005). In affective WM tasks, the neutral memoranda are replaced with 'standardized' affective stimuli that pertain to prototypical affective goals presumed to be more or less relevant to all participants (e.g., survival motives; Barrett, 2013; LeDoux, 2012). These can include words (Bradley and Lang, 1999), faces (Tottenham et al., 2009) and other affective images (Lang et al., 2008). Unfortunately, however, these stimuli are arguably low in affective significance (cf. approach and avoidance motivation; Elliot et al., 2013) for psychologically healthy individuals⁵ (Pessoa, 2009). That is, while these generic stimuli are still likely to receive some preferential processing within the cognitive system, their modulating effect on current task performance is proposed to be limited (Pessoa, 2009). At the behavioral level, this relatively weak impact on prioritization is likely to be both difficult to detect and replicate, as well as subject to strong influences from study specific factors such as WM load. Indeed WM for affective stimuli presented to healthy individuals shows mixed effects, with some studies showing an affective enhancement (e.g., Cromheeke and Mueller, 2016; González-Garrido et al., 2015), whereas others showing WM to be impaired for affective compared to neutral material (e.g., Meule et al., 2012; Rebetez et al., 2015); there are also some studies showing affective material to be remembered as easily as neutral material (e.g., Grimm et al., 2012; Tamm et al., 2017). Although these mixed effects support the notion of soft prioritization (Pessoa, 2009), suggesting that the stimuli used in laboratory research are low in affective significance, other explanations are also possible. For instance, using similar emotional standardized stimuli (e.g., pictures), studies of emotional episodic memory tend to report more systematic effects than studies of WM (Dolcos et al., 2011). This raises the possibility that it may be the nature of cognitive processes (episodic vs. working memory) that may be differentially susceptible to effects of emotion, rather than the properties of the stimuli themselves, that may influence their impact on cognitive performance when emotional information is task-relevant or task-irrelevant distraction, respectively (Dolcos et al.,

³ There are several competing theories of WM, generating vibrant debate around definitions and underlying mechanisms (cf. Miyake and Shah, 1999), which we acknowledge. An in-depth discussion of these debates, however, is beyond the scope of this review.

⁴ Although in this section we focus our discussion on the role of emotion in WM based on task relevance, it is also important to note here that other factors, such as those related to cognitive load and familiarity, have also been shown to influence WM and the associated mechanisms. For instance, greater WM load has been shown to attenuate processing of task-irrelevant negative distracters and the amplitude of the associated LPP (Hur et al., 2016; MacNamara et al., 2011). Moreover, greater familiarity with task-irrelevant distracters (e.g., faces of a loved one) has been linked to enhanced LPP amplitude, although it does not appear to significantly impair WM performance (Langeslag and van Strien, 2017).

⁵ Here, we focus on psychologically healthy individuals. Affective material, however, has been shown to have greater affective significance in individuals with mental health disorders. For a discussion of the role of attentional control in mental health difficulties including mood, anxiety, and stress-related disorders see below in sections 4 and 5.

2013). The latter may also be more susceptible to individual differences in the response to emotional distraction.

3.2.1.3. Neural effects. At the neural level, however, the effects of soft prioritization of standardized affective information should be easier to detect, because affective compared to neutral stimuli are proposed to have stronger perceptual representations in the brain's sensory cortices, especially the occipital cortex (Satpute et al., 2015). This increased strength of representation is reflected in augmented projections to the AMY leading to prioritized attentional processing within the brain's 'salience network' (Seeley et al., 2007; cf. ventral attention; Corbetta and Shulman, 2002). Greater direct processing of affective information, relative to neutral, in the fronto-parietal control network is a second source of variance which may be detectable at the neural level (Okon-Singer et al., 2015; Pessoa, 2009). However, given the dlPFC involvement in WM, affect-related differences are likely to be more visible in nodes associated with processing of affective competition in particular in the vlPFC and anterior cingulate cortex (ACC) (Bush et al., 2000; Iordan and Dolcos, 2017). In line with this proposal, the neuroimaging findings in healthy individuals appeared more consistent showing increased activation in the vlPFC, AMY, and sensory cortices in response to trials that require the maintenance of affective compared to neutral material in WM (Kerestes et al., 2012). However, Grimm et al. (2012) showed a pattern of decreased activation in the predicted regions and Perlstein and colleagues (Perlstein et al., 2002) showed dissociating effects of positive and negative material on dlPFC activation (see also next section).

In sum, affective WM appears to show relatively reliable neural recruitment of the ventral affective system (see also next section), yet in the laboratory behavioral effects are more mixed. Research is needed to investigate the association between affective WM paradigms used in the laboratory and affective WM capacity in real world environments (e.g., Pe et al., 2013a). WM tasks with affective material as distracters discussed below (e.g., task-irrelevant affective images; Dolcos et al., 2013) may constitute a closer approximation of the everyday contexts in which WM is commonly deployed.

3.2.2. Emotional distraction and working memory

In addition to its impact at the level of perception (see Section 2.2 above), the detrimental effects of task-irrelevant emotional distraction have also been investigated with respect to WM processes (reviewed in Iordan et al., 2013b; or affective sentences; Schweizer and Dalgleish, 2016). Of note, recent views in cognitive neuroscience identify selective attention and WM processes as largely overlapping or highly related constructs (Awh et al., 2006; Gazzaley and Nobre, 2012). Therefore, evidence regarding the role of distracting emotional information and how it affects the ability to temporarily maintain perceptual representations in mind bears particular relevance to the focus of this review. Models of affective-cognitive interactions inspired by clinical studies point to dysfunctional interactions between a dorsal executive neural system (DES) and a ventral affective system (VAS), and propose that impaired executive control and enhanced emotional distractibility observed in depression are linked to *hypofunction* of the DES and *hyperfunction* of the VAS (Drevets and Raichle, 1998; Mayberg, 2006). DES includes brain regions typically associated with executive functions, such as the dlPFC and the lateral parietal cortex (LPC), which are critical to active maintenance of goal-relevant information in WM. Increased activity in these regions during WM tasks is typically associated with increased task performance (D'Esposito et al., 2000; Miller and Cohen, 2001). VAS includes brain regions involved in emotion processing, such as the AMY, vlPFC, and mPFC (Lindquist et al., 2012; Vytal and Hamann, 2010).

Findings from recent studies investigating the neural correlates of cognitive interference by emotional distraction in healthy participants provide evidence that interactions between the DES and VAS are not only reflected in longer-lasting altered states, as observed in clinical

conditions such as depression, but can also occur transiently, in response to ongoing task-irrelevant emotional distracters. A series of studies by Dolcos and colleagues, investigating the neural correlates of processing emotional distraction, identified dissociable patterns of brain activity in the DES vs. VAS, which were specific to transient distracting emotions (Dolcos et al., 2008; Dolcos and McCarthy, 2006; Dolcos et al., 2007). The basic approach involved recording of brain activity using fMRI, while participants performed a delayed-response WM task with emotional distraction (see also Wong et al., 2012). The WM task involved keeping in mind a set of human faces (Memoranda) for the duration of a short delay, and then indicating whether a single face (Probe) was part of the initial set or not. During the delay interval between the memoranda and the probe, highly-arousing negative pictures were presented as task-irrelevant distracters. Participants were instructed to look at the distracters but maintain focus on the memoranda, and to make quick and accurate responses to the probes. Importantly, this task allowed clear dissociations of the time course of neural responses to emotional distraction in the DES and VAS as well as an objective quantification of the impact of emotional distraction on WM performance.

Using this paradigm, the study by Dolcos and McCarthy (2006) provided initial brain imaging evidence that impaired WM performance in the presence of emotional distraction is linked to increased activity in the VAS regions involved in emotion processing (e.g., AMY, vlPFC) while disrupting delay interval activity in the DES regions implicated in attentional processes and active maintenance of task-relevant information in WM (e.g., dlPFC, LPC). This opposing pattern of changes in VAS and DES activity was confirmed by significant region \times condition interactions (Dolcos and McCarthy, 2006). Importantly, the disruption of DES activation was associated with impaired WM performance. The results of this study are consistent with the idea that activity in the affective and executive neural systems is interconnected, such that increased activity in the VAS regions in the presence of transient emotional distracters temporarily takes off-line the DES and results in WM impairment, possibly as a result of a re-allocation of processing resources by emotional distraction (Dolcos and McCarthy, 2006).

These findings are consistent with the idea that the outcome of task-irrelevant emotional distraction depends on dynamic interactions between neural systems that allow the ability to stay focused on task-relevant information and systems involved in the processing of emotional information that may compete with the available processing resources. Possibly as a result of their salience, emotional distracters may produce a bottom-up impact on processing of goal-relevant information by re-allocating processing resources (Vuilleumier et al., 2001) and impairing performance. Although the exact nature of these resources is not clear, one possible interpretation is along the lines of Desimone and Duncan's (1995) biased competition model of selective attention, consistent with the idea that processing of emotional stimuli requires attentional resources, and that emotional stimuli compete for neural representation with all the other stimuli. Hence, the emotional distracters tap into the same resources necessary to process the task-relevant information, and impair WM performance. It is possible, however, that processing of emotional, especially threatening, information is prioritized, and hence it occurs automatically, without being limited by the availability of attentional resources (e.g., Anderson et al., 2003), as we discussed in previous sections.

More recent evidence also points to differential effects of positive and negative distraction and provides information about the timing of processing emotional distraction. Using an adaptation of the aforementioned WM paradigm, a recent study by Iordan and Dolcos (2017) has demonstrated that positive distraction had a reduced impact on WM performance compared to negative distraction. At the neural level, although processing of both positive and negative distraction was commonly associated with (arousal-driven) modulation of activity in the DES and VAS regions, these regions also showed dissociable activity by the valence of distraction. Specifically, processing of negative

distraction was associated with greater deactivation of the LPC (DES), whereas that of positive distraction was associated with greater activation of posterior vIPFC (Brodmann Area [BA] 9, VAS). Notably, activity in more inferior vIPFC (BA 45) was also positively correlated with WM performance under positive distraction (Jordan and Dolcos, 2017). Thus, reduced impact of positive distraction on WM performance is linked to both reduced impact on DES regions and increased engagement of VAS regions in coping with emotional distraction. Furthermore, common and dissociable effects of positive vs. negative distraction have also been identified in the temporal domain (García-Pacios et al., 2015). Together with the fMRI findings, these results point to possible spatial and temporal dissociations linked to the impact of vs. coping with emotional distraction in anterior lateral PFC/early time window vs. posterior lateral PFC/late time window, respectively (see also Dolcos et al., 2013).

3.2.2.1. Emotion-attention interactions linking the impact of distraction on working and episodic memory. Finally, similar to the evidence linking opposing effects of emotional distraction on perception and memory (Shafer and Dolcos, 2012), a study by Dolcos et al. (2013) linked opposing effects of emotion on WM (impaired) and episodic memory (enhanced). In particular, although AMY had a pivotal role in both effects, the impairing and enhancing effects of emotion were associated with greater dlPFC deactivation and HC activation, respectively. This suggests that task-irrelevant emotional distraction diverts processing resources from the main WM task (Dolcos and McCarthy, 2006), while initiating processing that leads to enhanced subsequent memory for the distracters themselves. Interestingly, trials producing enhanced episodic memory performance without disrupting WM performance were associated with increased vIPFC activity (Dolcos et al., 2013), possibly reflecting the engagement of mechanisms to cope with emotional distraction during WM, which then contributed to enhanced subsequent memory for the distracters.

In summary, studies investigating the neural correlates of the basic response to emotional distraction point to an interplay between two major neural systems: a ventral system (VAS), associated with emotional processing, showing increased activity, and a dorsal system (DES), associated with executive processing, showing decreased activity. The impact of task-irrelevant emotional distraction is chiefly supported by bottom-up mechanisms that may redirect processing resources away from the main cognitive task and toward stimuli with enhanced relevance for survival. Emerging evidence demonstrates that these mechanisms are also modulated by the valence of emotional distraction, with positive distraction being associated with reduced impact on the main task by virtue of increased engagement of coping mechanisms through posterior vIPFC. Negative distraction, possibly due to its greater WM interference, also seems to engage top-down control mechanisms involving specific regions of the dlPFC and vIPFC, as early as ~400 ms following the onset of distracters. Finally, the immediate impairing impact of emotional distraction on WM and the long-term enhancing impact of emotion on episodic memory appear to be mediated by overlapping and dissociable neural systems, involving bottom-up (medial temporal lobe [MTL]) and top-down (PFC) mechanisms.

3.3. Episodic memory

3.3.1. Basic fMRI evidence

Emotion has not only transient effects on cognitive processing, by influencing initial perceptual processes and attention paid to emotional stimuli or to details surrounding emotional events, but also long-lasting effects, which may eventually lead to better memory for those events. Vivid memories for emotionally charged personal events is anecdotal evidence supporting this notion, but there is also empirical evidence that emotional events are better remembered than neutral events (e.g., Bradley et al., 1992). Previous research has investigated the beneficial impact of emotion on long-term memory at various stages (reviewed in

Dolcos et al., 2012; Dolcos et al., 2017b), by typically considering two orthogonal dimensions of basic emotional properties, arousal and valence (Russell and Barrett, 1999). In addition, to minimize possible confounds related to general perceptual processing and to isolate memory-related neural mechanisms, brain imaging studies of emotional episodic memory typically calculate the so-called subsequent memory or difference due to memory (Dm) effects – that is, differential brain activity associated with remembered vs. forgotten items (Dolcos and Denkova, 2014; Dolcos et al., 2012; Shafer et al., 2011).

In general, current research mainly highlights the role of two mechanisms involved in the enhancing effect of emotion on episodic memory: (1) MTL-based mechanisms, involving the AMY and memory-related MTL regions, such as the HC and associated parahippocampal cortices, and (2) non-MTL mechanisms, involving PFC regions, among others (e.g., parietal cortex) (Dolcos et al., 2012). The MTL mechanism contributes to the memory-enhancing effect of emotion through direct/bottom-up neurohormonal interactions between the AMY and memory-related MTL regions, during encoding (e.g., Dolcos et al., 2004b), consolidation (McGaugh, 2004; Ritchey et al., 2008), and retrieval (Dolcos et al., 2005) of emotional memories. The non-MTL mechanism contributes to the memory-enhancing effect of emotion through indirect/top-down interactions, by enhancing semantic and executive processing, including attention (LaBar and Cabeza, 2006). Below, we discuss basic evidence regarding the role of these mechanisms during encoding and retrieval, based on fMRI studies.

3.3.1.1. Emotional memory encoding. Previous neuroimaging studies have identified the critical role of the interaction between the AMY and the memory-related MTL brain areas in successful encoding of emotionally arousing information (e.g., Dolcos et al., 2004b; Kensinger and Corkin, 2004), and showed that this within-MTL functional interaction is important for the persistence of emotional memories over time (Ritchey et al., 2008). More recently, it has been shown that encoding of emotionally arousing stimuli over an extended period (> 20 min) also induces a sustained arousal-related brain state (reflected in increased AMY-HC functional connectivity), which overall contributes to greater recollection of unrelated neutral items encoded minutes following the initial encoding of emotional ones (Tambini et al., 2017). This suggests that transient exposure to emotional arousal can also create persistent “carry-over” effects, resulting in similar memory-enhancing effects for subsequently-encountered neutral items (Fitzgerald et al., 2011; Hermans et al., 2014). Whereas AMY-MTL mechanisms are modulated primarily by arousal, the involvement of the PFC in emotional memory encoding seems to be influenced by valence (Dolcos et al., 2004a; Kensinger and Schacter, 2006). For instance, there is evidence that AMY-HC functional coupling tends to be enhanced for encoding of negative stimuli, whereas PFC-HC coupling is stronger for encoding of positive stimuli (Mickley Steinmetz et al., 2010; Ritchey et al., 2011b). In addition, there is also evidence showing that successful encoding of positive stimuli is associated with activation in frontal and parietal regions, whereas that of negative stimuli is associated with activation in temporal and occipital regions (Kensinger and Schacter, 2008; Mickley Steinmetz and Kensinger, 2009). This evidence lends support to other studies showing that encoding of positive information is related to activity in specific regions within the PFC (Dolcos et al., 2004a), likely due to increased processing requiring more cognitive resources (D'Esposito et al., 2000), whereas encoding of negative information is related to temporal and occipital areas (Mickley and Kensinger, 2008), likely due to enhanced sensory processing (Vuilleumier et al., 2004).

3.3.1.2. Emotional memory retrieval. Emotional retrieval has been mainly studied using two types of stimuli: (1) laboratory micro-events, such as a series of words or pictures, encoded in laboratory settings and retrieved at relatively shorter intervals following encoding (e.g., from minutes to months), and (2) autobiographical events,

referring to episodes from one's personal past, encoded in everyday life and usually retrieved after much longer intervals (e.g., years, decades). Similar to emotional encoding, previous studies provided evidence showing that successful emotional retrieval of laboratory micro-events involves the AMY-MTL mechanisms (Dolcos et al., 2005; Kensinger and Schacter, 2005). The AMY also seems to be involved in successful retrieval of emotionally arousing and personally relevant autobiographical memories (AMs), following shorter retention intervals (Muscatell et al., 2010). In addition, AMY's engagement during retrieval of more remote AMs seems to be dependent on task instructions associated with different levels of effortful processing (Smith et al., 2006), which may account for inconsistent findings regarding the AMY involvement in emotional AM retrieval (e.g., Vandekerckhove et al., 2005). Because the level of effortful processing is increased when remembering temporally dispersed past events, this could lead to diversion of attentional resources from the emotional value associated with recollection of such events (Phan et al., 2002). This idea has been supported by evidence from a recent study showing that attentional focus on emotional details (as opposed to non-emotional, contextual details) during recollection of emotional AMs was associated with increased activity in the left AMY (Denkova et al., 2013b). Also, similar to the evidence from encoding, AMY-MTL interactions also play a critical role in emotional retrieval, suggesting that the AMY and the memory-related MTL regions constitute a synergistic mechanism in which emotion and recollection enhance each other (Dolcos et al., 2005).

Importantly, retrieval-related functional interaction within the MTL also seems to be modulated by the PFC involvement. For instance, both increased AMY–HC connectivity and increased mPFC activity have been observed during emotional memory retrieval (Smith et al., 2006). Interestingly, the mPFC also modulated AMY and HC activity during retrieval of emotional information compared to that of non-emotional information. This result suggests that activity in the AMY can be modulated by task goals (Cunningham et al., 2008), and identifies the involvement of top-down processes linked to emotional memory retrieval subserved by the mPFC (see also Denkova et al., 2015). Finally, studies of memory retrieval for emotional laboratory (Smith et al., 2006) and autobiographical (Markowitsch et al., 2003) events have also identified the involvement of PFC regions linked to processing of emotional valence. In particular, increased medial and orbital PFC activity was identified during retrieval of positive contextual information and of positive AMs (Markowitsch et al., 2003). In addition, increased activity in the lateral PFC was associated with recollection of positive (but not negative) AMs while focusing on emotional details compared to non-emotional ones (Denkova et al., 2013a). The medial orbital PFC has been associated with affective valuation, reward-related processing, and self-referential processing (Heinzel and Northoff, 2009), whereas the lateral PFC has also been linked to the subjective experience of emotion (Wager et al., 2008), although given its functional heterogeneity (e.g., Petrides and Pandya, 2002) it is also associated with other aspects of emotion processing (e.g., emotion regulation, coping with distraction, Buhle et al., 2014; Dolcos et al., 2006). Taken together, these findings suggest that the involvement of specific medial/orbital and lateral PFC regions during retrieval of positive emotional information may reflect processing of self-relevant positive/rewarding experience (Dolcos et al., 2017b).

In sum, the evidence discussed above supports the notion that the memory-enhancing effect of emotion during encoding and retrieval is linked to increased engagement of and interaction among MTL and non-MTL (e.g., PFC) areas, involved in affective and mnemonic processes as well as other types of processing. While the MTL-based memory mechanism is relatively more involved in arousal-dependent effects, valence-related effects are linked to connectivity of these regions within and outside the MTL. Regarding the role of non-MTL regions, available evidence suggests that the involvement of PFC and other cortical areas (e.g., parietal) is relatively more sensitive to processing of valence and

reflects higher order processes (e.g., semantic and working memory, attention, cognitive control, and self-referential processing).

3.3.2. EEG/ERP evidence

Given its temporal resolution, EEG/ERP may be particularly relevant to unfold brief and early cognitive events (e.g., Pourtois et al., 2004; Schupp et al., 2003) related to the impact that emotion may have on encoding (e.g., Dolcos and Cabeza, 2002), consolidation, and retrieval processes (e.g., Schaefer et al., 2011; Weymar et al., 2009).

Similar to fMRI studies, EEG/ERP research on episodic emotional memory has mainly been focused on the modulatory effects of emotion on the processes related to memory encoding and retrieval, and less so on consolidation. Research focusing on encoding typically assesses changes in the brain dynamics by means of the subsequent memory/Dm effect. Research on retrieval usually assesses electrophysiological changes associated with the Old/New ERP effect (i.e., difference between correctly recognized old items and correctly identified new items, during recognition memory tests).

3.3.2.1. ERP correlates of emotional memory encoding. To date, the amount of ERP research focusing on the modulation on these processes by emotions is surprisingly scarce. In one of the first studies, Dolcos and Cabeza (2002) showed that, during an early epoch (400–600 ms), successfully remembered emotional pictures prompted a larger positive-going waveform than subsequently forgotten emotional pictures at central electrodes, an effect that was absent for neutral pictures. This ERP deflection had similar spatio-temporal characteristics to the LPP, a positive-going ERP usually observed during emotional picture processing that starts around 400 ms after stimulus onset over centro-parietal regions (e.g., Cuthbert et al., 2000). Because the LPP indicates sustained processing towards motivationally-relevant information (see for reviews, Hajcak et al., 2012; Lang and Bradley, 2010), the authors concluded that the enhanced memory encoding of emotional information reflects prioritized attentional processing that results in better subsequent memory (Dolcos and Cabeza, 2002; but see Galli and Otten, 2011). This interpretation is consistent with findings from studies using correlational approaches linking the amplitude of LPP response to better memory recall for emotional pictures (Palomba et al., 1997), indicating that attentional and elaborative processing leads to better memory formation for emotionally-relevant information (Weymar et al., 2012).

Similar results were observed in a more recent study using fearful facial expressions, which produced larger early (350–600 ms) Dm effects over central regions than neutral expressions (Righi et al., 2012) and overall available evidence suggests that memory for emotional stimuli benefits from enhanced attentional deployment towards emotional information but only when neutral information is present at the time of encoding (Wirkner et al., 2013; but see Schupp et al., 2012).

Finally, the enhanced processing for emotional information during encoding also predicts enhanced memory for source information associated with emotional events. In a recent study by Yick et al. (2015), at encoding, participants viewed a series of emotional and neutral scenes in two different blocks. Then, during retrieval, participants were presented with Old and New scenes and were asked to indicate whether they recognized the scenes and their origin (i.e., block 1 or block 2). Behaviorally, memory for emotional images and their location was better than for their neutral counterparts. At a neurophysiological level, correctly recognized emotional images generated a larger positivity than forgotten ones in a time window between 200 and 1500 ms, especially for the highly arousing pictorial information. Interestingly, when source information was correctly retrieved, larger Dm effects (400–1000 ms) were observed for emotional materials over anterior and posterior regions. This novel finding extends prior results indicating that emotional arousal not only facilitates the encoding of emotional items but also of associated source information (Yick et al.,

2015), leading to a robust long-lasting memory trace (see also discussion below on source memory ERP effects during retrieval).

Taken together, the ERP encoding results suggest that under limited capacity for neural representations (Bundesen et al., 2005), the set of processes involved in memory encoding prioritizes resources towards emotionally relevant information, at the cost of neutral non-relevant information (Watts et al., 2014; see for a review Mather and Sutherland, 2011). In turn, this leads to better memory formation for both emotional items and their associated source information.

3.3.2.2. ERP correlates of emotional memory retrieval. This section discusses evidence regarding both item and context memory. Regarding item memory, interestingly, the majority of the EEG research on emotional episodic memory has focused on ERPs during retrieval (see for review Weymar and Hamm, 2013; Weymar et al., 2009). A hallmark finding in this field is that correctly classified old items evoke an overall more positive-going ERP waveform than correctly classified new items (Rugg and Curran, 2007). This difference in ERP responses has been labeled as the ERP Old/New effect. Across a large number of studies using different stimulus material such as words (Maratos et al., 2000; Weymar et al., 2014), faces (Graham and Cabeza, 2001; Kissler and Strehlow, 2017), or scenes (e.g., Weymar et al., 2011, 2010), results have been mixed for the ERP Old/New effect for emotional and neutral contents, with some studies findings enhanced ERP Old/New differences, mostly over parietal electrodes indicating recollection, while others found no ERP differences as a function of emotionality. This discrepancy could be related to factors such as arousal or stimulus type, but also to differences in the retention interval used across studies (see Weymar and Hamm, 2013). In this sense, the retention interval and thereby sufficient consolidation (McGaugh, 2004; Yonelinas and Ritchey, 2015) has been shown to mediate the enhancing effect of emotion on episodic memories (Sharot and Phelps, 2004).

Whereas short consolidation periods (e.g. 3–5 min after encoding) result in comparable recognition rates for emotional and neutral items (Sharot and Phelps, 2004), longer delays (> 24 h) lead to a prominent memory advantage for emotional materials. This is because, with longer delays, recognition rates prevail for emotional items, but decline for neutral items (Ritchey et al., 2008). Similarly, during immediate retrieval tests, divergent ERP results have been often reported. In some studies larger ERP Old/New effects for emotionally arousing (both pleasant and unpleasant) items compared to neutral ones were observed (Langeslag et al., 2008), but in others these effects were absent (Weymar et al., 2013a). However, when memory is tested after long consolidation periods (> 24 h), enhanced late parietal Old/New differences have been reliably found for emotional items (e.g., Wirkner et al., 2015, 2018). Furthermore, ERP Old/New differences for emotional contents seem to be tremendously long-lasting over time. When memory for emotional and neutral materials is tested one year after encoding, emotional items are still better remembered than neutral ones (Dolcos et al., 2005; Weymar et al., 2011), which is also related to larger parietal ERP Old/New effects for emotionally arousing (especially unpleasant) items compared to neutral ones (Weymar et al., 2011).

Finally, more recent ERP memory studies revealed that the enhanced Old/New effect for emotional information occurs automatically, even when no intentional retrieval is instructed (Ferrari et al., 2013; Weymar et al., 2013a). These findings come from studies in which participants were engaged in non-memory-related tasks, involving free viewing (Weymar et al., 2013a), or active decision-making (Ferrari et al., 2013; Weymar et al., 2013a), while viewing old and new emotional and neutral images. Results showed that even when participants did not intend a memory search but view a memory cue, immediate retrieval was enhanced for emotional relative to neutral scenes, as reflected by enhanced parietal Old/New differences (Ferrari et al., 2013; Weymar et al., 2013a), suggesting that emotional scenes also trigger

recollection in a spontaneous fashion.

Besides item memory, one important aspect of human memory concerns the binding of contextual information (e.g., time, place, or associative cues) that constitutes many disparate features of a unified event (Davachi, 2006; Ranganath, 2010). In light of the relevance of such associative mechanism in our life, the question that arises is about what impact emotion exerts on memory for items as a part of, or in relation to, other items (Chiu et al., 2013). Despite abundant data showing enhancing emotional effects in item memory, the evidence regarding emotional influences on the accuracy of remembering contextual details is mixed (for reviews, see Chiu et al., 2013; Dolcos et al., 2017b; Weymar and Hamm, 2013). Similarly, ERP research investigating the effects of emotion on memory for associated neutral information has also yielded mixed findings (Jaeger and Rugg, 2012; Martínez-Galindo and Cansino, 2017). Recent ERP studies, however, indicate that one critical factor could be related to the retention interval (as for item memory), showing enhanced ERP Old/New differences for emotional, compared to neutral, associates when memory is tested one week after encoding (Ventura-Bort et al., 2017, 2016), but not when tested immediately or 24 h following encoding (Jaeger et al., 2009; Smith et al., 2004).

One other critical factor mediating potential modulatory effects of emotion on relational memory may be related to the binding strategy used during encoding (Mackay et al., 2004; Mather, 2007). According to the arousal-biased competition (ABC) theory (Mather and Sutherland, 2011), emotional arousal can lead to enhancement and impairment among neutral stimuli competing for attention depending on high or low priority (due to bottom-up perceptual salience or top-down attentional focus). The theory further suggests that emotional arousal may enhance associative memory for features of high priority items (e.g., color or location of an item) and impair memory for neutral items, when presented at the same time with emotional items. Thus, emotion can facilitate memory for intrinsically associated features of emotional stimuli (i.e. within-item associated details), but can also undermine memory for associated extrinsic cues (i.e. between-item contextual features) of the emotional information (Chiu et al., 2013; Mather, 2007). However, if the association between emotional cues and extrinsic neutral items is well integrated, memory for neutral items may improve due to the acquisition of high priority. These issues are the focus of an emerging debate in the literature on emotional memory (Dolcos et al., 2017b; see also Ventura-Bort et al., 2017; Weymar et al., 2014).

3.3.2.3. Oscillatory correlates of emotional episodic memory. Finally, besides ERPs, research has increasingly focused on the role of neuronal oscillation and synchronization on episodic memories (see for a review Nyhus and Curran, 2010), emphasizing the role of gamma (25–100 Hz) and theta (4–8 Hz) oscillations on the formation and retrieval of episodic memories (Nyhus and Curran, 2010). For instance, several studies observed that successful encoding is associated with greater gamma power and gamma synchronization (e.g., Gruber et al., 2001; Sederberg et al., 2007), and that theta and gamma oscillations support retrieval processes (Ferrari et al., 2015; Summerfield and Mangels, 2005). However, most of the evidence indicating that these synchronizations mediate emotional memory retrieval comes from animal research (e.g., Pare et al., 2002), and thus more research in humans is needed (Gärtner and Bajbouj, 2014).

Taken together, ERP results showed that memory retrieval is enhanced for emotional stimuli and associated neutral information with high attentional priority, as reflected by enhanced ERP Old/New differences. This memory advantage is likely driven by HC-mediated recollective processes, which as for item memory may be most robust following longer consolidation intervals. In addition, despite overall mixed findings, there is also evidence that emotional information also enhances memory for contextual details. Regarding the oscillatory correlates, available data indicate that theta and gamma oscillations in

the MTL and cortical regions are involved in the formation and retrieval of episodic memories, which in synchronization with the AMY contribute to the generation of emotionally relevant episodic memories.

Notably, attention, learning, and memory are also critically affected by stress. Stressors initiate various bodily adaptation processes to re-establish physiological homeostasis and promote long-term well-being by interacting with emotional and cognitive processes. Therefore, although not the focus of the present review, it should be noted that stress induction is also a way of manipulating responses and influencing emotion-attention interactions⁶. These stress-induced alterations are thought to be involved in the development, establishment, and maintenance of various stress-related disorders, such as post-traumatic stress disorder (PTSD), and of other emotional disturbances (anxiety, depression), which are discussed further in the following sections.

4. Individual differences in emotion-attention interactions

In the field of emotion processing, individual differences are the norm rather than the exception (Hamann and Canli, 2004). Hence, when assessing emotional reactions, individual differences should be examined rather than being regarded as statistical noise (Kosslyn et al., 2002; Phan et al., 2003). Because such differences can affect aspects of processing that are relevant to understanding clinical conditions, the present section discusses the role of a wide range of individual differences that influence emotion processing – from developmental (at both early and later stages) and sex to personality and clinical differences linked to various disorders (anxiety, depression, and PTSD).

4.1. Developmental differences

4.1.1. Early stages: childhood and adolescence

4.1.1.1. Emotional distraction. The ability to resist interference from distracting emotional information while sustaining attention on goal-directed behavior is critical for adaptive behavior. Using “classic” cognitive control tasks such as the flanker (Grose-Fifer et al., 2013), Stroop and Go/No-Go (Tottenham et al., 2011), several studies have examined age-related differences in interference from distracters that include socially- and/or emotionally-relevant information, such as facial expressions or emotional words (e.g., Cohen-Gilbert and Thomas, 2013; Grose-Fifer et al., 2013). Most studies have focused on childhood and adolescence, with a few focusing on infancy and preschool age. A linear decrease in interference from such distracters from childhood into adulthood has been documented by some studies (Somerville et al., 2011; Tottenham et al., 2011). For instance, Tottenham et al. (2011) examined the performance of children (5–12 years old), adolescents (13–18 years old), and adults (19–28 years old) using a block design emotional Go/No-Go task, and showed that performance improved with age. Nevertheless, across the age groups, false alarms occurred more frequently to emotional relative to neutral face No-Go stimuli, which were interpreted as indexing reduced inhibitory control in the context of emotionally salient emotional information. Using a similar version of the task in the MRI scanner, Hare and colleagues documented elevated AMY activation in

adolescents relative to children and adults on this task (Hare et al., 2008). Furthermore, elevated AMY and reduced vIPFC activation positively correlated with slower RTs to the fearful (versus happy) face target stimuli. Functional connectivity analyses revealed that the strength of AMY-vIPFC coupling was correlated with greater habituation of AMY activity to fearful face targets in adolescence (Hare et al., 2008). Such findings have been interpreted in terms of neurodevelopmental changes in neural systems supporting cognitive control into the adult years (Bunge et al., 2002; Rubia et al., 2006).

Other studies, however, have reported a curvilinear developmental pattern, with emotional distracters showing the greatest influence on task performance during adolescence (e.g., Cohen-Gilbert and Thomas, 2013; Grose-Fifer et al., 2013). For instance, studies examining developmental changes in emotional interference found that adolescents (aged 11 to 19 years) showed greater interference to negative compared to positive and neutral emotional conditions on an emotional Go-NoGo task (Cohen-Gilbert and Thomas, 2013), and to fearful compared to happy faces on an emotional Flanker task (Grose-Fifer et al., 2013). This curvilinear pattern has been attributed to a maturational gap between subcortical regions supporting emotion processing, which has been characterized as highly-reactive, and still-maturing prefrontal cortical regions supporting cognitive control and regulatory processes (Casey and Galvan, 2016). Consequently, adolescents are more likely to show a preferential processing for social and emotional information (Monk et al., 2003; Nelson et al., 2005), which is posited to underlie an adolescent-specific peak interference from emotional distracters and adolescents’ increased vulnerability to affective disorders.

Recognizing the limitations of rather simplistic models based primarily on immaturity of prefrontal cortical regions, a third developmental pattern pertaining to the development of neural systems supporting the interactions between cognitive, emotional, and social processing has been observed, whereby neural activation in prefrontal cortical regions supporting cognitive control increases during mid-adolescence (Crone and Dahl, 2012; Geier et al., 2010). Researchers interpret this pattern as evidence of increased task engagement during adolescence and suggest that there are some contexts (e.g., peer interaction or reward seeking) in which adolescents might recruit greater cognitive control than adults or children, thereby showing less cognitive interference. This pattern is also consistent with developmental models highlighting adolescence as an important period for socio-affective learning (Crone and Dahl, 2012; Schriber and Guyer, 2016).

4.1.1.2. Emotional memory. Unlike the well-documented memory-enhancing effects of emotion in adulthood (LaBar and Cabeza, 2006), relatively little is understood to date about how emotional memory develops and whether this is present early in development or changes over time (Hamann and Stevens, 2013). Understanding the development and integration of emotion and memory systems advances our understanding of typical emotional memory development and maladaptive memory processes, such as overgeneral memory formation which is associated with a range of mental health problems (Dalgleish and Werner-Seidler, 2014). The literature on emotional memory in children comes from naturalistic investigations as well as from a growing body of more controlled laboratory experiments. Evidence from memory for actual events shows that children, like adults, remember emotional events better than neutral ones (Ackil et al., 2003; Goodman et al., 2010). For example, children who lived through a tornado were more likely to remember the event than other neutral events (Ackil et al., 2003). Nine years after the tornado children who were youngest at the time of the event remembered the greatest proportion of emotional versus neutral events with the proportion decreasing with age (Bauer et al., 2017). Laboratory evidence shows a similar pattern (Vasa et al., 2011), although not all studies show an emotional enhancement effect (Leventon and Bauer, 2016) and some even showed reduced memory for emotional material (Howe et al., 2010).

⁶ Existing literature covers the complex effects of stress on processes such as attention, learning, and memory, and the temporal actions of two major stress mediators, in particular catecholamines and glucocorticoids (Henckens et al., 2009; Hermans et al., 2014; Joëls et al., 2011; Schwabe and Wolf, 2014; Solstad et al., 2006; van Ast et al., 2013; Weymar et al., 2013b, 2014; Weymar et al., 2012). Furthermore, given that stress mediates both initial and subsequent stages of processing influencing learning and memory, from increased vigilance to retrieval, pharmacological interventions or new neurostimulation methods (transcutaneous vagal nerve stimulation, Van Leusden et al., 2015; Ventura-Bort et al., 2018) that target either or both stress systems at these stages of processing might be useful for future prevention and treatment (de Quervain et al., 2017).

The absence of an enhancement effect observed in some studies has been proposed to reflect an emergent integration of memory and emotion systems across development. In support of this, [Leventon et al. \(2014\)](#) reported an absence of enhanced recognition performance in both younger (5–7.5 years), and older (8–9 years) groups. The older group, however, showed event-related potential during the recognition of negative memoranda that was distinct (enhanced LPP for negative items) from neutral items ([Leventon et al., 2014](#)). Functional neuroimaging of emotion memory in young people has shown the recruitment of the same neural substrates in the AMY-HC complex, the inferior temporal lobe, and the ACC ([Krauel et al., 2007](#); [Nelson et al., 2003](#); [Vasa et al., 2011](#)). However, subtle differences exist when comparing patterns of activation with adults, including greater AMY activation and more wide-spread activation during the encoding of emotional information ([Nelson et al., 2003](#); [Vasa et al., 2011](#)). It should be noted, however, that no studies included children younger than 9 years and the samples were small.

Together, these studies suggest that emotion-attention interactions and underlying neural substrates undergo important maturational changes in childhood and adolescence. Most of the findings, however, have been documented using cross-sectional designs and, as such, there remains a need to replicate these results using longitudinal follow-up studies that assess changes in behavior as well as neural structure and function. Children, compared to adolescents and adults, tend to exhibit greater interference to emotional distracters. They also tend to exhibit enhanced memory for emotional compared to neutral events. Studies examining the connectivity between PFC regions supporting cognitive control processes suggest that short-range connections tend to become weaker with age, whereas long-range connections, which are important for integration across networks, become stronger with age ([Fair et al., 2007](#)). Thus, it is possible that underlying attention, memory, and emotion systems may become more integrated and parsimonious across development into adulthood.

4.1.2. Later stages: aging

Aging is not only associated with well-known co-morbidities and losses but also with relatively high levels of emotional well-being. Considerable evidence supports the idea of an age-related positivity effect in emotional attention, perception, and memory, by which older adults tend to (a) pay greater attention to, process, and remember more positive information, and (b) show reduced processing of negative information compared to younger adults ([Mather, 2016](#); [Reed and Carstensen, 2012](#)). According to the Socioemotional Selectivity Theory ([Reed and Carstensen, 2012](#)), older adults' preference for positive over negative information is driven by their prioritization of more present-focused motivational goals related to emotional meaning and satisfaction, which in turn enhances their well-being. This suggests that age-related differences in emotion processing occur as a function of differential engagement of the top-down mechanisms, such as emotion regulation strategies, that allow older adults to spontaneously cope with emotional challenges ([Dolcos et al., 2014](#); [Mather and Carstensen, 2005](#)). As discussed below, available evidence regarding the neural correlates of age differences in emotion-cognition interactions points to relatively preserved bottom-up (AMY) mechanisms and enhanced top-down (PFC) mechanisms.

4.1.2.1. Age-related differences in emotion perception. Supporting the idea that age differences in emotion processing are primarily linked to modulation of top-down/controlled mechanisms, there is evidence suggesting that bottom-up/automatic processing of emotional stimuli is relatively preserved in aging ([Dolcos et al., 2014](#); [Katsumi et al., 2019b](#); [St Jacques et al., 2010](#)). Such preservation of sensitivity to basic emotional information in aging has been most consistently associated with similar engagement of AMY in young and older adults, which also seems to show less structural decline as a function of age compared to other brain regions (e.g., [Jiang et al., 2014](#)). In the context of overall

preserved AMY functioning in aging (which is particularly sensitive to high arousing/threatening stimuli), there is also evidence showing age differences in AMY sensitivity to the valence of stimuli. Previous studies of emotional perception identified decreased AMY response to negative stimuli ([Iidaka et al., 2002](#); [Mather et al., 2004](#)) or increased AMY response to positive stimuli ([Kehoe et al., 2013](#); [Mather et al., 2004](#)), in older compared to young adults.

Furthermore, increased engagement of the mPFC and ACC regions during the viewing of negative vs. neutral and positive vs. negative stimuli has also been reported in older adults ([Dolcos et al., 2014](#); [Nashiro et al., 2012](#); [St Jacques et al., 2010](#)). These findings, along with evidence for chronic activation of emotion regulation goals in aging ([Gross et al., 1997](#)), suggest that greater activity in the mPFC/ACC regions linked to emotional perception may reflect enhanced habitual engagement of emotion regulation strategies in older adults, which may further exert modulation of activity in basic emotion processing regions (AMY). Consistent with this idea, there is evidence for increased functional connectivity between the ACC and AMY in healthy older adults, who also show overall lower emotional ratings of negative stimuli ([St Jacques et al., 2010](#)). This idea was further supported by recent evidence identifying activity in similar mPFC/ACC areas showing a negative association with subjective emotional ratings for negative stimuli in older adults ([Dolcos et al., 2014](#)), thus confirming a role of this region in effective spontaneous regulation of negative emotions in aging (see also [Dolcos et al., 2017a](#)). Notably, this study also clarified that the observed effects were specific to processing of low arousing stimuli, thus highlighting the importance of taking into consideration the level of emotional charge when investigating emotion processing in aging.

4.1.2.2. Age-related differences in emotional distraction and memory. Differences in emotion processing in older adulthood also extend to differences in emotional distraction and emotional memory. Regarding emotional distraction, consistent with a positivity bias in emotion processing, evidence suggests that older adults are less easily distracted by negative emotional stimuli compared to younger adults ([Mather, 2012](#)). For example, in an emotional Stroop study, younger adults were slower in naming the color of neutral words that followed negative words, while older adults did not show this effect ([Ashley and Swick, 2009](#)). Another study showed that, when asked to identify a target number displayed over a distracter face, younger adults were most distracted by angry faces, while older adults were most distracted by happy faces ([Ebner and Johnson, 2010](#)). Additionally, a recent study found that older adults in a positive mood induction group showed enhanced memory for previous distraction compared to those in a neutral mood group ([Biss et al., 2012](#)). Consistent with previously mentioned evidence on the neural correlates of emotional perception in aging, fMRI evidence from older adults have shown greater ACC engagement in response to irrelevant positive faces than irrelevant neutral faces when attention to the central face location was high, whereas this pattern was not found in younger adults ([Brassen et al., 2011](#)). Regarding emotional memory, both younger and older adults showed the memory enhancement by negative information, although this effect was larger in the former group ([St Jacques et al., 2009](#)). At the neural level, consistent with the behavioral effect and also with the literature on emotion perception, both age groups showed greater AMY activity associated with subsequent memory for negative vs. neutral stimuli. Moreover, the same study also identified increased and decreased activity in the dlPFC and visual cortex, respectively, in older adults linked to subsequent memory for negative vs. neutral pictures. These findings are overall consistent with existing models of cognitive aging (e.g., Posterior-Anterior Shift in Aging; [Davis et al., 2008](#)), and suggest that greater PFC activity associated with older adults' emotional encoding might reflect enhanced engagement of spontaneous emotion regulation.

Finally, there is also evidence that older adults have greater susceptibility compared to younger adults to the aforementioned memory

trade-off effect between emotional/central vs. non-emotional/peripheral aspects of an event (Kensinger et al., 2007; Nashiro and Mather, 2011). These age-related differences have been associated with older adults' relatively decreased tendency to engage in particular encoding strategies (e.g., broad allocation of attention to contextual features of stimuli) that help younger adults reduce the negative influence of the trade-off effect. This suggests that older adults may have particular difficulty in disengaging attention from emotionally salient features of stimuli (Kensinger et al., 2007, 2005). Furthermore, there is evidence that emotional arousal enhances memory for information about intrinsically-linked contextual aspects (e.g., stimuli and their location) through memory binding in younger adults but not in older adults, thus suggesting that possibly limited cognitive resources in older adults may lead them to remember only the gist but not the associated details (Nashiro and Mather, 2011).

In summary, available evidence suggests that emotion-attention interactions and the associated neural substrates are altered throughout childhood, adolescence, younger and older adulthood. Children tend to show greater interference by emotional distracters compared to adolescents and adults, and enhanced memory for emotional compared to neutral events. Older adults tend to show a positivity bias in perceiving emotional information, in the context of preserved emotion processing. This results in reduced distraction by negative emotional stimuli and diminished impact of negative valence on emotional memories. In addition, there is also greater susceptibility to the memory trade-off effect between emotional/central vs. non-emotional/peripheral aspects of events, compared to young adults. At the neural level, children tend to show greater AMY activation along with more wide-spread activation while processing emotional information, whereas older adults tend to show decreased AMY response to negative stimuli and increased response to positive stimuli. These basic emotion processing responses are coupled with increased responses in regions associated with cognitive control of emotion (PFC and medial frontal/ACC regions) during emotion processing, particularly of negatively-valenced stimuli, which also influences emotional distraction and emotional memory. These findings highlight emotion-attention interactions across the life span, as well as the associated interactions between bottom-up (AMY) and top-down (PFC/ACC) neural mechanisms.

4.2. Sex differences

4.2.1. Emotional attention and perception

In our society, it is commonly believed that women perceive, experience, and express emotions to a greater extent than men do (Briton and Hall, 1995; Meyers-Levy and Loken, 2015). This section discusses scientific evidence pointing to both beneficial and detrimental aspects related to the role of sex differences in emotion processing. Consistent with the beneficial aspects, there is evidence pointing to *enhanced emotional competence* in women compared to men (Collignon et al., 2010; Hall and Matsumoto, 2004). Women pay more attention to, as well as identify and decode others' emotional expressions more accurately (Collignon et al., 2010; Hall and Matsumoto, 2004), are more emotionally expressive (Kring and Gordon, 1998), and display more extensive knowledge of emotional experience (Barrett et al., 2000) than men. However, there is also evidence highlighting *increased vulnerability* to affective disorders in women, who are known to exhibit enhanced reactivity to emotional stimuli, particularly negative ones (Hamann and Canli, 2004; Spalek et al., 2015). In addition, women tend to be more cautious and show avoidance-focused motivations (Meyers-Levy and Loken, 2015), which may be linked to nearly two times higher lifetime prevalence of mood and anxiety disorders than in men (Bekker and van Mens-Verhulst, 2007; Kessler, 2003).

At the neural level, available findings identify both general and specific sex differences in the patterns of brain activations during emotion processing, and provide evidence consistent with a *negative affective bias* in emotion processing in women. A recent meta-analysis of

brain imaging studies examining sex differences identified a sex \times valence interaction in emotion processing, such that women are more likely to show greater AMY response to negative information, whereas men tend to show greater AMY response to positive information (Stevens and Hamann, 2012). Moreover, a subsequent study by Andreano et al. (2014) showed that AMY response to negative stimuli tends to be "persistent" over multiple repetitions in women, whereas AMY response to negative stimuli in men is only sensitive when the stimuli are novel (as opposed to familiar). This finding lends support to the idea that reduced habituation of AMY response to negative stimuli may be linked to the greater incidence of affective disorders in women (Andreano et al., 2014).

Interestingly, previous brain imaging studies of sex differences have also identified patterns of hemispheric lateralization in brain activity linked to emotion processing (Killgore and Yurgelun-Todd, 2001; Williams et al., 2005), as well as differential sensitivity to contextual factors. For instance, compared to women, men showed greater activity in the right AMY during an emotional face perception task (Schneider et al., 2011), and similar lateralization differences in AMY activity have also been identified in the memory domain (Cahill et al., 2001; Canli et al., 2002; see also the next section). Furthermore, additional evidence regarding sex-related hemispheric lateralization effects has been identified by studies examining ERP responses, in which the authors found an asymmetrical activation of the visual cortex between men and women during an emotional face judgment task, characterized by right hemisphere-dominant P1 and N1 responses in men compared to women (Proverbio et al., 2006).

In sum, available evidence concerning sex differences in the effect of emotion points to women's enhanced sensitivity to emotional stimuli in general, and to negative stimuli in particular. Although women generally exhibit enhanced emotional competence in emotion processing, compared to men, they are also more likely to show a negative affective bias in attention and perception. At the neural level, women's negativity bias in emotional perception has been linked to increased sensitivity in the bottom-up emotion processing regions including the AMY, which may, in turn, be linked to heightened vulnerability to emotional disturbances in women. Evidence also points to the existence of hemispheric lateralization linked to emotion processing, with men and women typically exhibiting enhanced activity in the right vs. left hemisphere, respectively.

4.2.2. Emotional distraction and emotional memory

4.2.2.1. Sex differences in emotional distraction. Possibly linked to the increased susceptibility to affective disorders in women compared to men (Bekker and van Mens-Verhulst, 2007; Kessler, 2003), women also show enhanced reactivity to emotional challenges (Hamann and Canli, 2004; Shields, 1991) and specificity in the deployment of emotion regulation strategies (Denkova et al., 2012; Mcrae et al., 2008). Given the possibility that the same mechanisms that help generate the enhanced emotional experience in women could also be partially responsible for enhanced sensitivity to emotional challenges, in a recent investigation Iordan et al. (2013a) examined whether sex differences in basic emotional reactivity are also associated with differences in emotional distractibility.

First, consistent with the idea of increased bottom-up impact of emotional distraction in women relative to men, women showed increased sensitivity to emotional distraction in brain regions associated with emotion processing, such as FG and AMY. Supporting the idea of enhanced bottom-up effects in women, the left FG, a perceptual area susceptible to modulation by emotion, showed increased activity in response to angry-face distracters in female participants as well as a negative correlation with WM performance. Increased response to emotional distraction in women relative to men was also identified in the subgenual ACC, a higher-level emotion integration region, which has been linked to the experience of negative emotion, in both healthy and clinical samples (Baeken et al., 2010; Mobbs et al., 2009). These sex

differences in the basic response to emotional distraction are consistent with increased sensitivity in ‘bottom-up’ responses in women, linked to impaired WM performance. However, they were identified in the context of overall similar brain response to emotional distraction in women and men, suggesting that, at a more general level, men and women also deploy similar mechanisms in response to emotional distraction. Second, the same investigation also identified sex differences in coping with emotional distraction. Results revealed a dorsal-ventral hemispheric dissociation within the lateral PFC, with the left ventral PFC being linked to individual differences in WM performance in women, and the right dorsal PFC being linked to individual differences in men. Interestingly, the same left vPFC region showing enhanced activation in the female participants who performed better in the WM task (Denkova et al., 2010) showed ‘by default’ overall increased level of activity in males, who also had overall higher levels of WM performance.

Overall, these results support the idea that enhanced emotional competence in women may have the side-effect of increased emotional reactivity, which in turn may lead to enhanced emotional distractibility. This brain imaging evidence points to sex differences in both bottom-up and top-down effects of emotional distraction, by linking increased recruitment of emotion processing areas with decreased cognitive performance in women and by revealing dissociations between women and men in the mechanisms of coping with distraction. Hence, investigating the role of sex differences that mediate both basic responses to and the ability to cope with emotional challenge offers a promising path for better understanding differential susceptibility to affective disorders in women and men.

4.2.2.2. Sex differences in emotional memory. There is also evidence that women display more extensive knowledge of emotional experience (Barrett et al., 2000) and recall more emotional autobiographical memories (Davis, 1999; Seiditz and Diener, 1998) than men do. Complementing the evidence discussed above, neuroanatomical research also revealed sex differences in emotion-related brain regions (e.g., AMY and orbitofrontal cortex volumes) (Goldstein et al., 2001; Gur et al., 2002). Consistent with behavioral and neuroanatomical evidence suggesting differences between men and women, evidence from brain imaging studies also pointed to sex differences in the involvement of the AMY in emotional memory (e.g., Andreano and Cahill, 2009; Hamann, 2005). One such notable difference points to hemispheric asymmetry in the role of the AMY in emotional memory encoding (e.g., Cahill et al., 2001; Canli et al., 2002), with left AMY being associated with successful emotional memory encoding in women and right AMY being associated with successful emotional memory encoding in men (but see Fischer et al., 2007). Interestingly, this hemispheric lateralization seems to be confined to the basolateral AMY, and observed following a longer (2 weeks) but not shorter (minutes) retention interval (Mackiewicz et al., 2006), which suggests that this lateralization is influenced by memory consolidation processes (see also Talmi et al., 2008). Further investigation of sex differences in AMY’s involvement during emotional memory encoding suggests that feminine and masculine roles as established by the society, rather than the sex *per se*, seem to influence these differences in emotional memory (Cahill et al., 2004).

Overall, the evidence regarding sex differences in emotional memory points to hemispheric differences in the role of the AMY during emotional memory encoding and consolidation, and suggests that taking into account the social dimension and gender-specific societal roles is of particular interest in understanding differences between women and men (Cahill et al., 2004).

4.3. Personality and clinical differences

The impact of emotion on attentional processes appears to occur differently across the population. To comprehensively take such

variability into account, it is important to investigate aspects such as personality differences and clinical status. Personality neuroscience is an emerging field that contributes to clarifying aspects regarding the role of personality differences in understanding vulnerability and resilience to emotional dysregulation (Canli, 2004; DeYoung et al., 2010), with important implications for understanding both healthy and clinical functioning. Here, we focus on two of the most well-documented personality traits, anxiety and depression, that not only modulate how emotional stimuli compete for our attention, but also in their own right seem to disrupt aspects of the attentional system. These traits are also the target of emerging interventions discussed in Section 5, and of models and theories that show how individual differences in other domains, such as regulatory focus, are associated with indicators of well-being (Eddington et al., 2007, 2009; Higgins et al., 2012; Llewellyn et al., 2013). Other personality traits (extraversion, neuroticism) can also influence emotion processing and its interactions with executive functions (Canli, 2004; Forster et al., 2015; Rohr et al., 2015), but are not the focus of the present discussion.

4.3.1. Trait anxiety

A hallmark characteristic of individuals with high anxiety (either as a trait factor of high nervousness/worry, or at a clinical level) are selective biases within attention towards emotional information, specifically threat-laden content (Dudeny et al., 2015; Okon-Singer et al., 2011). For example, anxious individuals have difficulty ignoring threat-denoting distracter words in emotional Stroop tasks (Williams et al., 1996), as well as angry/fearful faces in dot probe paradigms (e.g., Rudaizky et al., 2014). Moreover, this bias extends beyond the allocation of attention to the level of WM: anxious individuals appear to prioritize visual WM capacity towards encoding threat-laden content, even if it is task-irrelevant, at the expense of other information to memorize (Stout et al., 2015, 2013). Both children and adults with anxious disposition, like many patients with anxiety disorders, tend to excessively allocate attention to threat-related cues when they are present in the environment, even when they are irrelevant to the task at hand (Bar-Haim et al., 2007; Dudeny et al., 2015).

Such findings have led to numerous theoretical accounts positing that these biases relate to automatic facilitation of attention towards threat in anxiety (see Cisler and Koster, 2010). This is also supported by neuroscientific evidence that threat detection and processing is typically reflected in increased neural activity within the AMY (e.g., Davis and Whalen, 2001), and that anxious individuals similarly show increased AMY response to threat-related distracter stimuli (e.g., Bishop et al., 2007). Finally, there is some evidence that emotional biases in attention seen amongst anxious individuals may in fact causally relate to the development of anxious symptomatology. As discussed in the last section, recent cognitive intervention methods, such as attentional bias modification (ABM) training, have shown that attentional biases to threat can diminish as a result of training individuals to divert their attention away from threat-laden stimuli in the visual environment. Additionally, it has been found that self-report levels of anxiety also attenuate as a result of such training (see MacLeod and Mathews, 2012), suggesting that, while attentional biases in anxiety are seen as a classic symptom, they may also relate as a root contributing factor to anxious disposition.

While anxiety appears to exacerbate some of the emotional biases in attention in relation to threat, anxiety in its own right also appears to modulate the attention network. Across a range of selective attention measures, anxious individuals show heightened distractibility by task-irrelevant stimuli, suggesting an impaired inhibition function (e.g., Berggren and Derakshan, 2013b, 2014). Supporting this, neuroscientific investigations have shown that anxious individuals recruit areas of the PFC associated with attentional control differently compared to low anxious individuals during tasks requiring distracter inhibition (e.g., Basten et al., 2012). Findings such as these are accommodated within the influential Attentional Control Theory (ACT) (Eysenck et al., 2007),

which proposes that anxiety may impair three key functions of attentional control: inhibition, flexible shifting between tasks, and updating of information within WM (Miyake et al., 2000). In addition, this reduction in top-down control of attention may increase the bottom-up saliency of other information, hence resulting in high difficulty to maintain goal-focused attention.

An open question is whether evidence of reduced attentional control in anxiety can explain why such individuals also show enhanced biases to threat-related information? Growing neuroscientific evidence suggests that both functional and structural connectivity between prefrontal areas involved in attentional control and limbic areas related to emotional responses is reduced in anxious populations (e.g., Kim et al., 2011). Moreover, cognitive training interventions targeting attentional control efficiency have produced both reductions in attentional control impairments in anxiety and attenuated self-report feelings of worry (Sari et al., 2016).

In summary, anxiety appears to differentially influence attention and its relationship with emotion. On the one hand, accumulating evidence shows that attentional control is disrupted in high anxiety, while conversely emotion processing appears enhanced particularly in relation to threat. Supported by neuroscientific work, these findings suggest a trade-off between the efficiency of prefrontal brain regions associated with attentional control vs. relatively enhanced response within the limbic and sensory network related to threat detection. Much progress has been made particularly in targeting these two networks through ABM and attentional control training to reduce anxious symptomatology, and combined dual-pronged training approaches may provide promise against a backdrop where current cognitive-behavioral treatments of anxiety typically report an efficacy rate of only 30–50% (Taylor et al., 2012).

4.3.2. Trait depression

Within depressed groups, including those of high trait dysphoria, rumination, and clinical depression, emotional interactions with attention appear to more generally encompass attentional biases to negative information than the relatively threat-specific idiosyncrasies of anxiety. Individuals with high depressive symptoms show difficulty ignoring and rejecting negative information (e.g., De Raedt and Koster, 2010; Joormann, 2004), which has been proposed to explain why such individuals typically experience depressive symptoms due to a simple difficulty in rejecting such thoughts and behaviors (Joormann, 2004). As with anxiety, however, impaired ability to ignore distraction also occurs for non-emotional material across clinically depressed and at-risk groups (e.g., Beckwe et al., 2014; Owens et al., 2012). Such findings have led to similar emphasis on attentional control as in anxiety (e.g., Koster et al., 2017). Moreover, neuroscientific evidence has similarly shown that depression links to aberrant neural response in areas of PFC linked to attentional control (e.g., Davidson et al., 2002), increased AMY response to presented negative stimuli (e.g., Siegle et al., 2007b), and reduced connectivity between these areas when viewing such images (e.g., Almeida et al., 2009). Finally, as in the case of anxiety, cognitive interventions targeting attentional control in depressive groups have demonstrated improvements in regulating negative emotional material (e.g., Iacoviello et al., 2014), as well as some evidence of reductions to self-reported depressive symptoms following active training (Segrave et al., 2014). Such methods provide promise as new intervention techniques for depression where current treatments fall short given high remittance rates within clinical practice (e.g., over 20%; Driessen et al., 2013).

In summary, at the clinical level, anxiety and depression typically have a high comorbidity rate (Hirschfeld, 2001), and research examining emotion-attention interactions within these populations highlight clear similarities in the potential mechanisms underlying the role of these characteristics. Whether specifically for threat or negative events in general, emotion consumes and perhaps also compromises attention, while poor attention may equally play a causal role in the

ability to regulate such emotions. This interplay has led to promising developments in cognitive interventions targeting these mechanisms, although with regimens often focused on emotional regulation or attentional control in isolation. Consideration of the reciprocal links between emotion and attention in relation to personality factors may yield new insight and opportunities for ameliorating chronic negative affect within the general population.

4.4. Clinical anxiety and depression

A growing number of studies have documented alterations in the functioning of fronto-limbic systems supporting modulation of attention to emotional information in individuals diagnosed with or at risk of developing anxiety or depression. There is growing evidence that attentional biases or stimulus-driven attention toward or away from specific emotional information could contribute to the onset and prevalence of these disorders (Jacobs et al., 2008; Lau and Waters, 2017). Attentional bias emerges through heightened activity in limbic regions (e.g., AMY, insula) signaling the need to modulate cortical regions (e.g., ACC, TPJ). If the information is irrelevant to their current goal or context, goal-directed attention, supported by PFC areas (dlPFC, mPFC/ACC, orbitofrontal cortex), re-directs or maintains attention to task-relevant stimuli (Pessoa, 2017). Although attentional biases to threat-related information have been primarily associated with anxiety (Cisler and Koster, 2010), biased attention to negative stimuli is also characteristic of depression (Peckham et al., 2010).

Regarding anxiety disorders, cognitive theories have put forward different accounts to explain attentional biases to threat, some suggesting a bias toward or away from threat-related information (Kaufman et al., 1997), whereas others highlight the role of cognitive control processes in the monitoring and regulation of attention (Derryberry and Reed, 2002). There is agreement, however, that such alterations could be both a vulnerability factor that leads to the development of anxiety disorders (Bar-Haim et al., 2007) and an important contributing factor to the maintenance of anxiety disorders (Williams et al., 1997). Consistent with this idea, perhaps the most systematic finding in individuals with clinical anxiety (Monk et al., 2008) links individual differences in anxiety to negative coupling of frontal and AMY regions (i.e., fronto-AMY connectivity). Turning to depression, extensive research has also revealed patterns of emotional biases in basic cognitive processes, also known as cognitive biases in depression (Gotlib and Joormann, 2010). These include attentional and memory biases whereby there is increased processing of negative information at the expense of neutral and positive information (Gotlib and Joormann, 2010; Winer and Salem, 2016). Cognitive (Beck, 1967) and emotional theories (Clark, 2005) maintain that individuals who are experiencing depression and who are at risk for the disorder exhibit attentional biases, whereby they preferentially attend toward negative stimuli and away from positive stimuli in their environment (Joorman et al., 2007; Owens et al., 2016). The next sections discuss evidence regarding such biases in clinical anxiety and depression.

4.4.1. Visual perception and working memory in clinical anxiety

Although individual differences in the way we experience our surroundings are normal, extremely biased perception may be dysfunctional in psychopathology. Evidence shows that individuals with clinical anxiety manifest perception biases when presented with threatening stimuli compared to non-threatening ones. For example, participants with high levels of acrophobic symptoms were asked to estimate the height of a balcony while they stood on a high building themselves. Highly fearful participants estimated the balcony to be higher than the less fearful participants. Notably, the less fearful participants also overestimated the height (Teachman et al., 2008), suggesting a general perception bias that might be related to biological preparedness (see Aue et al., 2016, 2013, for similar findings related to attention bias to spiders among participants with low fear levels). A

similar bias was shown in state anxiety – in a different study (Stefanucci et al., 2008), participants were asked to stand on a skateboard (which was shown to provoke fear) or on a stable wooden box (control group) on top of a hill and to estimate the steepness of the hill. Individuals standing on a skateboard estimated the hill as steeper than those standing on a wooden box. A related kind of perception bias was shown in arachnophobia. For example, Vasey et al. (2012) asked spider-phobic participants to estimate the size of a spider and concluded that size estimation biases correlate with the level of fear of spiders, so that the higher the phobia from spiders was, the larger the spider was perceived. Together, these findings demonstrate that estimation bias exists both when anxiety is acute and when it is dispositional, and it is exacerbated in clinical anxiety. Perception biases may be related to other well-documented processing biases, such as attention, expectancy, interpretation and memory biases. However, the correlational and causal relations between them are unclear, although both attention and perception biases are thought to affect early stages of processing. Further research is also needed to clarify the neural mechanisms that mediate perceptual biases.

Turning to WM, individuals with, or even those who are prone to, emotional disorders such as anxiety and depression, present an exaggerated effect of inefficient gating of threat from WM (Stout et al., 2013) that disrupts endogenous attention and other control mechanisms. Specifically, when anxious individuals are asked to encode information into WM, both non-affective and threat-related distracters interfere with performance. The heightened negative affect (i.e., anxiety, sadness) characterizing these populations may be partially explained by this deficit (Cohen et al., 2014; Stout et al., 2017). For example, anxious individuals tend to experience invasive thoughts and distress, even when the threat is utterly irrelevant to the current task or even when it is not present in the external environment, perhaps due to allocation of excess storage capacity to real or imagined threat (Shackman et al., 2016). When threat-related information penetrates into WM, it distorts information processing (i.e., attention, memory retrieval, and response), thus promoting rumination, worry, and other dysfunctional cognitions (Thiruchselvam et al., 2012).

Notably, influences between cognition and emotion are bi-directional (Dolcos and Denkova, 2014; Dolcos et al., 2011; Dolcos et al., 2017a; Okon-Singer et al., 2015), and thus there are tight links between WM and current emotional states that are manifested in overlapping brain circuits involved in attention and WM, that are also crucial for emotion regulation (Etkin et al., 2015). For example, cognitive reappraisal, a prevalent strategy for emotion regulation, requires effortful maintenances of explicit regulatory goal and depends on a WM circuit including the lateral PFC and posterior parietal cortices (Buhle et al., 2014). Consistent with this notion, individual differences in WM capacity are predictive of reappraisal success (Etkin et al., 2015). Furthermore, mood-congruent representations are activated in WM during negative mood, arousing persistent negative thoughts, selective attention to negative stimuli and biased recall and processing of negative memories (Rolls, 2013; Siemer, 2005). When humans attempt to regulate and repair their negative mood, they do so by trying to control the content of WM by elaborating more positive thoughts and memories. These attempts fail in populations with emotional disorders, and thus their deficient ability to control WM results in a “self-defeating cycle” of increasingly negative thinking and intensifying negative affect (Joormann, 2010).

4.4.2. Attentional/executive control in depression

Depression is a highly debilitating affective disorder which is characterized by sustained negative affect and anhedonia. Cognitive symptoms typically include patterns of negative thinking about the self, the world, and the future, as well as disturbances at the level of cognitive processes such as memory, concentration, and attention (American Psychiatric Association, 2013). Although disturbances at the level of cognitive processes have oftentimes been considered secondary

features of negative mood, theories of depression increasingly consider them to be a major factor that contributes to the maintenance and exacerbation of depressive symptoms (Disner et al., 2011; Millan et al., 2012). Typically two classes of disrupted cognitive processes are distinguished in the context of depression: cognitive biases and general attentional/executive control (see Gotlib and Joormann, 2010). Below we briefly describe each of these disturbances in more details.

Cognitive biases refer to the tendency to selectively process negative affective information over neutral or more positive information. Cognitive biases have been investigated at the level of attention, interpretation, and memory. Past studies have used behavioral tasks (e.g. Emotional Stroop, Dot Probe, and Posner Cueing task), as well as eye tracking paradigms to examine attentional processing of affective information in depression. Overall, these studies seem to suggest that later, but not early, attentional processes are impaired in depression (for a review see De Raedt and Koster, 2010). More specifically, depression is associated with impaired disengagement from negative, self-referential information, and depressed individuals also pay less attention to positive information than non-depressed individuals. Interestingly, several prospective studies have shown that such attentional biases are associated with slower recovery from stress (Sanchez et al., 2013) and sustained negative mood (Clasen et al., 2013). Interpretation biases have been investigated with a wide range of different tasks, where typically ambiguous information is presented and researchers assess whether this information is interpreted systematically in a positive or a negative manner (see Hirsch et al., 2016). A recent meta-analysis of this body of research (Everaert et al., 2017b) showed that depression is associated with a tendency to interpret information in a more negative manner. However, this was only found on measures relying on self-report, but not on tasks with more implicit dependent variables (RTs or psychophysiological responses). Finally, memory biases are the most well-established biases in depression, with evidence pointing to better explicit memory for negative information (Matt et al., 1992), and there is also evidence of overgeneral autobiographical memory in depression (Williams et al., 2007).

Moreover, an extensive body of work examined more general executive functions in depression. Although there is quite a bit of heterogeneity among different individual studies, a recent meta-analysis indicates that depressed individuals show broad deficits in a host of tasks measuring executive functions (Snyder, 2013). Cognitive theories of depression have argued that various aspects of executive functioning (switching, inhibition, and updating) are impaired in depression, which influences the capacity to regulate emotions (Joormann and Vanderlind, 2014). These ideas have received some empirical support (Everaert et al., 2017a, b). Interestingly, there is also emerging research that examines the causal influence of executive functions on depression and emotion regulation. Several studies have shown that extensive training of cognitive control can reduce levels of rumination and depressive symptoms (see Koster et al., 2017). This research is described in more detail below (section 5). Despite a large body of studies establishing an association between depression and executive functions, less research has been devoted to the origins of impaired performance on tasks measuring executive functions. Moreover it is unclear how motivational factors, that are assigned a key role in basic models of cognitive control (Botvinick and Braver, 2015), play a role in depression-related cognitive impairments (Grahek et al., 2018).

4.5. Trauma- and stress-related disorders

As discussed in the preceding sections, emotion can either enhance or hinder various aspects of our cognition and behavior. For instance, the emotional charge of an event can increase attention to and memory for that event (Dolcos et al., 2017b), whereas task-irrelevant emotional information may lead to increased distraction away from goal-relevant tasks (Iordan et al., 2013b). Changes in affective and cognitive processing are critical features in PTSD patients, typically reflected in

increased emotional reactivity and recollection of traumatic memories, along with impaired cognitive/executive control (Rauch et al., 2006; Shin and Liberzon, 2009). This section focuses on emerging evidence linked to the role of specific emotion regulation strategies whose altered interactions with attentional processes seem to be central to the PTSD symptomatology. Of particular importance is also emerging evidence concerning the impact that such alterations have on the way emotional memories (Hall et al., 2018; Hayes et al., 2011) and emotional distraction (Morey et al., 2009) are processed in PTSD, and on the associated neural mechanisms (Dolcos, 2013).

4.5.1. Attentional control, emotion regulation, and PTSD

Emotion regulation deficits are commonly observed in those who experience symptoms of post-traumatic stress (for a review see Seligowski et al., 2015) and emotion regulation capacity predicts the onset and maintenance of post-traumatic stress symptoms following trauma, as shown in several prospective studies using self-report measures of emotion regulation in young people (Jenness et al., 2016; Punamäki et al., 2015), as well as psychophysiological measures of emotion regulation during a behavioral emotion regulation task in veterans (Fitzgerald et al., 2018). Differences in emotion regulation capacity also appear to be good predictors of treatment response to both psychological (e.g., prolonged exposure therapy) and psychopharmacological (e.g., selective serotonin reuptake inhibitors) interventions (Jerud et al., 2016; MacNamara et al., 2016). Despite this accumulating evidence, there is no unified theory of the role of emotion regulation in the development and maintenance of PTSD.

Regarding attentional control in PTSD, given this review's focus on the interplay between affective and attentional processes, we explore the role of attentional control in the association between emotion regulation capacity and PTSD. Attentional control has been proposed as a top-down control mechanism (Eysenck et al., 2007) that overrides implicit biases in attentional processing that favor threat-related information in those at risk for anxiety-related problems (Bar-Haim et al., 2007). Self-reported attentional control (Derryberry and Reed, 2002) has been associated with fewer post-traumatic stress symptoms over a 1–3 month interval in individuals who experienced a stressful event during this period (Bardeen et al., 2015). Behavioral measures of attentional control show a more complex relation with PTSD, through the impact of attentional control on attentional biases. A study in trauma-exposed college students showed threat-related attentional bias, measured as the time spent looking at threatening images when presented with neutral/threat pairings, to be predicted by the interaction between self-reported attentional control and levels of post-traumatic stress symptoms (Bardeen and Orcutt, 2011). Individuals with high levels of both attentional control and symptoms of post-traumatic stress dwelled less on threatening images, but not individuals low in attentional control and symptoms of PTSD. The authors interpreted these findings as evidence for the adverse effects of habitual avoidance of negative information. Interestingly, Schoorl et al. (2014) showed the exact opposite pattern of results in patients with PTSD who completed the dot-probe task as a measure of attentional bias. Attentional bias on the dot-probe was measured as the relative latency in response to probes that appeared in the location of threatening versus non-threatening images. The results showed that individuals low in attentional control and high in PTSD symptoms showed an attentional bias for threatening information, whereas those with medium-high attentional control did not.

A meta-analysis of emotional Stroop (including trauma-related or general negative threat stimuli) as a measure of attentional bias toward threat in PTSD showed that individuals with PTSD demonstrated impaired performance in response to trauma-related stimuli compared to both trauma exposed controls without PTSD and individuals who never experienced a trauma (Cisler and Koster, 2010; for more recent evidence including the neural substrates of the emotional Stroop effect in PTSD, see Herzog et al., 2017). Support for an attentional control deficit

in PTSD stems from two findings within this meta-analysis. First, threat words only impaired Stroop performance in studies with unmasked but not with masked stimuli, with the former requiring a certain degree of elaboration and effortful processing and thus attentional control. Second, effects were stronger in studies with blocked designs, where slow inter-trial effects that depend on attentional control can emerge. The causal influence of attentional control on the development and maintenance of PTSD symptoms, however, remains poorly understood. A recent study suggested that rather than poor pre-trauma attentional control constituting a risk factor for the development of PTSD, trauma exposure may lead to dysregulated attentional processing (Schäfer et al., 2018). The same group, though, found that pre- and post-deployment attentional bias, as an index of deficits in attentional control, was associated with symptoms of PTSD in soldiers (Schäfer et al., 2016). Together, these findings provide preliminary support for a role of attentional control in PTSD through its impact on attentional biases, but the temporal and directional nature of this association warrants further investigation.

Turning to the link between attentional control and emotion regulation, any attentional control effects in PTSD are likely to operate on the different stages of the emotion regulation process (Gross, 2015; see section 5.1). Early stage effects arguably operate when attention is deployed toward non-threatening information and away from threat eliciting cues (Shvil et al., 2013). This avoidance of trauma-related information may come at the cost of increased re-experiencing and related distress (Bomyea and Lang, 2016; Mäirean and Ceobanu, 2017). Good emotion regulation capacity and the attentional control it relies on, in turn, are required later in the emotion regulation process to effortfully regulate unwanted intrusions and their associated distress (Bomyea and Lang, 2016). For example, Bomyea and Lang showed that in sexual trauma survivors with low executive control (measured by a complex span task argued to rely on attentional control; Kane et al., 2001) avoidant thought regulation strategies were associated with persistent intrusions, whereas they were not in trauma survivors high on control capacity. Problematically, the general reduction in executive control capacity (Aupperle et al., 2012), and attentional control in particular (Flaks et al., 2014), observed in PTSD appears to hinder the habitual implementation of adaptive emotion regulation strategies, such as cognitive reappraisal (Karatzias et al., 2018; Shepherd and Wild, 2014). However, when individuals were experimentally instructed to use cognitive reappraisal to regulate their emotions in response to negative stimuli, refugees with high levels of post-traumatic stress symptoms experienced fewer intrusions in the following two days than those who had been instructed to suppress their affective responses. Similarly, studies comparing groups with and without PTSD on behavioral measures of emotion regulation capacity in response to images presented in the laboratory have shown no group differences in the ability to down-regulate affective responses (Fitzgerald et al., 2017; Woodward et al., 2015). Together, these studies suggest that PTSD may not be associated with deficient emotion regulatory capacity *per se*, but in combination with attentional control deficits, habitual selection of adaptive strategies in daily life becomes impaired.

Interventions targeting these deficits in attentional control capacity have shown promising preliminary results both as stand-alone interventions (Badura-Brack et al., 2015; Schweizer et al., 2017) and as adjuncts to existing interventions for PTSD (Kuckertz et al., 2014). In support of a mechanistic association between emotion regulation and control capacity, Schweizer et al. (2017) showed that training attentional control over emotional information in adolescents with PTSD improved not only symptoms of PTSD but also self-reported use of positive emotion regulation strategies. Moreover, training adaptive strategies such as reappraisal may also be effective, as suggested by a study using a trauma analogue film paradigm (Woud et al., 2012). In sum, the evidence reviewed here supports an interacting role of attentional control and emotion regulation capacity in the onset and maintenance of post-traumatic stress symptoms. Importantly, these

effects may be harnessed to develop easy to disseminate, computerized training interventions to reduce suffering in those who experience symptoms of post-traumatic stress in the aftermath of trauma exposure.

4.5.2. Emotional memory and emotional distraction in PTSD

Sometimes the opposing effects of emotion on cognition (enhanced emotional memory vs. increased emotional distraction) co-occur. For example, hearing a gunshot may capture our attention and distract us from ongoing activities. In turn, such increased distraction by task-irrelevant emotional stimuli may lead to better memory for the distracting information itself and, if that incident had a powerful effect on us, such memories can become intruding later on. The co-occurrence of enhancing and impairing effects of emotion is probably most evident in affective disorders, where both of these opposing effects are exacerbated. For instance, uncontrolled recollection of and rumination on distressing memories observed in PTSD may also lead to impaired cognition due to enhanced emotional distraction. This section discusses evidence regarding alterations of the neural mechanisms associated with emotional memory and emotional distraction in PTSD, with a focus on regions involved in episodic and working memory (i.e., MTL and dlPFC, respectively). Links between emotional memory and emotional distraction in PTSD are also discussed.

Regarding emotional memory, neurobiological models of PTSD (Layton and Krikorian, 2002) propose that the development and maintenance of the disorder is linked to altered activity in the MTL during encoding of traumatic memories. Hence, intrusive recollection of traumatic memories observed in PTSD may be linked to dysfunction of the basic MTL mechanism identified in healthy participants as being responsible for the memory-enhancing effect of emotion (Dolcos et al., 2004b). Specifically, processing of cues related to traumatic events may trigger recollection of traumatic memories, which due to dysfunctional interactions between AMY and the MTL memory system may engage a self-sustaining functional loop in which emotion processing in AMY may enhance recollection by increasing activity in HC. This, in turn, may intensify AMY activity as a result of re-experiencing the emotions associated with the recollected memories (Dolcos et al., 2005). On the other hand, there is also evidence suggesting a disconnect between the effects observed in AMY and their link to emotional or cognitive aspects of processing in PTSD patients. Specifically, whereas greater AMY activation is identified in studies of symptom provocation (Rauch et al., 2000; Shin et al., 2004), such an effect is not observed in studies of cognitive processing (Admon et al., 2018; Morey et al., 2008).

An important observation that has emerged in the PTSD literature may reconcile this apparent discrepancy. Specifically, there is evidence that memories for negative events in PTSD patients may be non-specific, gist-based, rather than detailed, context-based (Harvey et al., 1998; McNally et al., 1994). Gist refers to familiarity-based retrieval of memories for the general meaning of a situation or event, rather than recollection of specific contextual details (Tulving, 1985). Given that gist-based memories are often inaccurate (Roediger and McDermott, 1995; Wright and Loftus, 1998) and susceptible to enhanced rate of false alarms that may diminish or cancel an actual enhancing impact of emotion on memory (Dolcos et al., 2005), it may be the case that the basic AMY-MTL mechanisms typically responsible for the memory-enhancing effect of emotion are in fact attenuated in PTSD. Hence, this could explain the non-specific, gist-based, memories observed in these patients. This idea is supported by recent findings from an fMRI study using the subsequent memory paradigm with emotional stimuli in PTSD patients (Hayes et al., 2011), which showed reduced memory-related activity in the AMY-MTL system during memory encoding, and higher false alarm rates during retrieval, compared to a trauma exposed control (TEC) participants. Moreover, the PTSD patients also lacked the anterior-posterior dissociation along the longitudinal axis of the MTL, with respect to its involvement during successful encoding of emotional memories, which was initially identified in healthy participants (Dolcos et al., 2004b), but such dissociation was preserved in the TEC group

(Hayes et al., 2011). Taken together, these findings suggest a disorganization of the MTL mechanisms involved in the memory-enhancing effect of emotion in PTSD, which leads to inefficient encoding of information for trauma-related stimuli and subsequent non-specific gist-based retrieval (Dolcos, 2013).

Regarding emotional distraction, studies investigating the neural correlates of the impairing effect of task-irrelevant emotional distraction on cognitive performance identified distinct patterns of responses in emotion and cognitive control brain regions (i.e., increased activity in AMY and reduced activity in dlPFC, respectively), which are specific to emotional distraction (Iordan et al., 2013b). On the one hand, based on this evidence, increased emotional reactivity linked to changes in the AMY function in PTSD may lead to increased specific disruption of dlPFC activity by emotional distraction. On the other hand, there is evidence for a non-specific heightened sensitivity to both threatening and non-threatening stimuli in PTSD (Grillon and Morgan, 1999), which may explain increased distractibility to trauma related and unrelated stimuli alike.

The fact that information unrelated to the trauma may also be highly distracting in PTSD patients is consistent with the clinically observed symptom of hypervigilance in these patients, and with the evidence for non-specific encoding of trauma-related material discussed above (Hayes et al., 2011). Specifically, it is reasonable to expect that seemingly neutral stimuli that may remind of trauma could act as cues for non-specific retrieval of trauma-related information, which in turn may be as distracting as the trauma-related stimuli themselves. Evidence from a recent study of WM with trauma-related and non-related distraction is consistent with this idea (Morey et al., 2009). Using an adaptation of our WM task with emotional distraction (Dolcos and McCarthy, 2006), the study by Morey and colleagues investigated how trauma-related task-irrelevant emotional information modulates WM networks in PTSD. Similar to the study on memory encoding discussed above, recent post-9/11 war veterans were divided into a PTSD group and a TEC group. fMRI results showed that the PTSD group had greater trauma-specific activation than the control group in main emotion processing brain regions, including the AMY and vlPFC, as well as in brain regions susceptible to emotion modulation (e.g., FG). However, the PTSD group also showed greater non-specific disruption of activity to both combat-related and neutral task-irrelevant distracters in brain regions involved in the maintenance on goal-relevant information, including the dlPFC. This suggests a more generalized dlPFC disruption in the PTSD than in the control group, which showed only disruption specific to the trauma-related distraction. The non-specific dlPFC response to combat vs. non-combat distracters in PTSD is consistent with the hypervigilance hypothesis that may explain enhanced response to neutral stimuli. This neural-level finding was complemented by the behavioral results, which showed lower overall WM performance for task-irrelevant distracters scenes in the PTSD group, in the absence of a differential impact between combat-related and neutral distracters.

4.5.3. Linking emotional memory and emotional distraction in PTSD

Overall, the evidence from the two separate lines of investigations discussed above, regarding the neural changes in PTSD linked to dysfunctions in the recollection of traumatic events and the response to emotional distraction, converge toward the idea that non-specific responses to emotional and neutral distraction may reflect retrieval distortions linked to inefficient initial encoding of trauma-related information. Namely, it is possible that the non-specific disruption of the dlPFC activity by trauma-related and neutral distraction is linked to the retrieval of the traumatic memories triggered by non-specific cues, which may also contribute to the perpetuation of the state of hyperarousal observed in these patients. Moreover, it is also possible that the source of these effects is linked to elevated arousal during the initial exposure to traumatic events. Consistent with this idea, in addition to showing non-specific activity to subsequently remembered items in AMY and the MTL memory system in PTSD, the study by Hayes and

colleagues discussed above (Hayes et al., 2011) also identified a negative co-variation of memory-related HC activity for trauma-related items with scores of hyperarousal symptoms, as measured with the Clinician-Administered PTSD Scale. In other words, participants who had greater hyperarousal scores also had reduced memory-related activity during the encoding of trauma-related pictures. This finding is consistent with evidence for an inverted U-shaped function in the HC as a function of stress (Nadel and Jacobs, 1998) and provides a possible explanation for the non-specific effects observed in the tasks assessing emotional memory for trauma-related cues and their undifferentiated impact on goal-relevant processing when presented as task-irrelevant distraction. Consistent with the role of the initial arousal in these effects, PTSD patients also showed relatively greater activity for forgotten items, which may be linked to AMY hyperactivity leading to later forgetting of those items (Hayes et al., 2011).

In summary, available evidence from investigations of PTSD patients points to general and specific emotional and cognitive disturbances that are linked to alterations in the neural circuitry underlying emotion-cognition interactions, and specifically linked to attention. This evidence suggests that reduction of AMY and HC signals for trauma-related cues may underlie non-specific encoding of gist-based representations instead of specific and detailed contextual details of the trauma-related memories. This, in turn, may be linked to symptoms of hypervigilance and non-specific responses to trauma-related distraction, which contribute to the maintenance of a hyperarousal state. This evidence also highlights the importance of investigating both the enhancing and the impairing effects of emotion to understand the changes associated with affective disorders, where both effects are intensified (Dolcos, 2013). Collectively, these findings point to the importance of investigating both of these opposing effects of emotion within the same clinical group, to complement similar approaches in healthy participants concomitantly investigating the enhancing and impairing effects of emotion on cognitive processes (Dolcos et al., 2013; Shafer and Dolcos, 2012).

5. Training and interventions to optimize emotion-attention interactions

Neuroplasticity, the idea that the brain is plastic, is not entirely new, but one that recent research is capitalising on for its potential to positively influence mental health and well-being (Kays et al., 2012). When we learn new information, consolidate old information into new, and plan for the future, our brain is constantly generating new neural connections, and regenerating old neural connections as it sees relevant. Neuroplasticity is an exercise that the brain does naturally, to adapt to new situations, adjust, and change according to situational demands. It is the fuel for resilience, the art of adapting smartly, to survive (Kays et al., 2012). The emotional and cognitive brain systems rely on neuroplasticity to communicate with each other flexibly to attain behavioral outcomes (Pessoa, 2017). Emotional systems are instrumental for our survival, from detecting signs of danger to experiencing basic emotions such as sadness, joy, pain, and fear, to more elaborate emotions such as gratitude, grief, and grit. Cognitive systems, on the other hand, are programmed to manage and regulate our emotions. They fuel the brain to regulate emotions, harmonise, and generate appropriate responses, and help us make decisions (Pessoa, 2013). Hence, effective communication between emotional and cognitive brain systems is incredibly important for sustaining cognitive and emotional health, and for succeeding in both every day and more challenging tasks. Provided the intricate relation between cognition and emotion, it has been argued that a strict distinction between these two systems is problematic (Pessoa, 2017).

Because of the intertwined nature of affective and cognitive processes, it is reasonable to imagine that changing aspects in one domain may affect information processing in the other. For instance, reducing one's sensitivity to emotional stimuli will also influence the way they

impact cognitive processes, such as attention, perception, and memory. On the other hand, similar effects can be obtained by improving one's ability to exert top down control on the way emotional stimuli are processed. Hence, this section emphasizes the dual relations between emotion and attention, as it is not only the case that emotions influence attention but cognitive training of attention also influences emotion processing. Following an introduction of evidence linking attentional control, working memory, and emotion regulation, this section discusses emerging evidence about how training and interventions can optimize emotion-attention interactions.

5.1. Executive/attentional control and emotion regulation

Executive functioning refers to a set of processes, such as WM and selective attention, necessary for monitoring behaviors that facilitate the attainment of goals. Emotion regulation is defined as the automatic and volitional processes that determine an individual's affective experience (Gross, 2002). These processes vary in the extent to which they depend on executive control operations: inhibition, WM updating, and set-shifting (Friedman and Miyake, 2017). In their seminal paper on the cognitive control of emotion, Ochsner and Gross (2005) defined control as ranging from attentional control to cognitive change, where attentional control refers to attention selection toward or away from affective information depending on its motivational properties (Pourtois et al., 2013), and cognitive change encompasses the application of higher cognitive abilities including WM and long-term memory to emotion regulatory processes. More recently, Braunstein et al. (2017) have expanded on this to operationalize emotion regulation strategies along a second dimension. In addition to considering emotion regulatory processes' demands on executive control ranging from primarily automatic to controlled processes, this extended framework further considers the nature of the emotion regulatory goals: explicit versus implicit. Here, we focus on emotion regulation processes that rely on executive control, where explicit regulation processes include regulation strategies such as reappraisal (Buhle et al., 2014) and cognitive distraction (Moyal et al., 2014), whereas implicit regulatory processes refer to automatic affective control observed on affective versions of the Stroop and Go/No go tasks (Schmeichel and Tang, 2015; see also Wager and Atlas, 2015); see also Braunstein et al. (2017), for evidence about automatic regulation processes that require little cognitive control resources.

5.1.1. Explicit emotion regulation and working memory

Several meta-analytic reviews of explicit emotion regulation strategies provide robust evidence for brain networks involved in attention control (Buschman and Kastner, 2015) and WM (Nee et al., 2013), in particular the lateral PFC, to be recruited for successful emotion regulation (Buhle et al., 2014; Ochsner et al., 2012). The majority of the literature is focused on reappraisal or non-specific down-regulation. In the latter participants are required to down-regulate their emotions, but they may be engaging in any number of emotion regulatory strategies (e.g., attentional deployment, distraction, reappraisal) that will vary in terms of their demands on control resources. With the exception of Buhle et al. (2014), who focused exclusively on reappraisal, this hinders conclusions with regard to specific emotion regulation strategies. Interestingly, despite this relatively extensive neuroscientific literature, there is less experimental work directly probing the association between executive control capacity and emotion regulation. Preliminary evidence from the WM literature shows that individuals with high WM capacity appear better at both voluntary and spontaneous emotion regulation (McRae et al., 2012; Schmeichel and Demaree, 2010), although Gyurak et al. (2012) failed to show this association in healthy individuals and individuals suffering from neurodegenerative disorders. Critical prospective studies suggest that these individual differences in WM capacity interact with stressful exposure to predict mental health functioning (Pe et al., 2016; Quinn and Joormann, 2015). Arguably the

mechanism through which WM capacity influences mental health outcomes is through emotion regulation. That is, lower WM capacity during stress leaves less resources for the deployment of adaptive regulation strategies.

Outside the laboratory, recent advances have provided further support for the role of WM in emotion regulation. For example, in an experience sampling study (N = 95), Pe and colleagues (Pe et al., 2013b) showed that affective WM updating ability predicted individuals' ability to down-regulate high-arousal negative affective states (e.g., experiencing anger), but not low-arousal negative affective states (e.g., dysphoria). Finally, preliminary evidence suggests that emotion regulation may be improved by WM training. That is, training WM for emotional material improved both implicit (Schweizer et al., 2011) and explicit emotion regulation (Schweizer et al., 2013). The gains in reappraisal capacity following affective WM compared to placebo training were mediated by changes in lateral PFC activation during the affective WM task as well as behavioral improvement in affective WM (Schweizer et al., 2013). Together these findings highlight the sparsity of empirical evidence investigating the association between explicit emotion regulation and executive control in general and WM in particular. The available evidence also suggests that good WM capacity is critical to successful emotion regulation.

5.1.2. Implicit emotion regulation and attentional control

Braunstein et al. (2017) dissociated between two types of implicit emotion regulation. The first operates in the context of another task where affective experiences are regulated to successfully complete another task. That is, the emotion regulatory goal here is incidental to the overarching task goal. The second type of implicit emotion regulation refers to emotion regulatory efforts triggered by implicitly activated (cf. primed goal states) regulation goals. For a review of the latter, see Bargh and Williams (2007), as it is beyond the scope of this review. The first type of implicit emotion regulation is critical for everyday functioning by inhibiting attention toward task-irrelevant affective information (e.g., phone alerts) when performing another task. In the laboratory, affective attentional control is typically measured with emotional Stroop (Phaf and Kan, 2007) and affective Go/No-Go (Schulz et al., 2007) tasks (see section 3.2 for affective working memory tasks). These tasks are again associated with increased recruitment of the lateral PFC as well the mPFC and dorsal ACC (Braunstein et al., 2017; Etkin et al., 2011). Individual differences in affective attentional control are associated with a range of functional outcomes related to mental health. Poor affective attentional control as measured by greater interference from negative material on the affective Stroop task is related to biased attention toward negative information in anxious individuals and those suffering from anxiety disorders (Bar-Haim et al., 2007). Poor inhibition of prepotent affective responses as measured by the emotional Go/No-Go task has also been observed in both bi- and unipolar mood disorders (Phillips et al., 2008). Importantly, evidence from the developmental literature shows that these deficits in attentional control (cf., effortful control; Eisenberg et al., 2014) are prospectively associated with mental health, including externalizing and internalizing symptoms (e.g., Han et al., 2016).

In sum, both explicit and implicit emotion regulation appear to vary as a function of individual differences in executive control capacity. The neural substrates underlying successful emotion regulation include the lateral PFC and extend to the mPFC and dorsal ACC for implicit emotion regulation.

5.2. Introduction to executive control training

Deficits in executive control and cognitive biases harm the well-being of those affected, impacting the way they pay attention to, interpret, and remember information, and play a key role (either causal or contributory) in the onset, maintenance, and possibly the recurrence of/recovery from these conditions (Power and Dalgleish, 2015).

However, accumulating evidence suggests that attentional biases and executive functions are plastic and can be altered by early and adult life experiences or interventions (Bar-Haim and Pine, 2013; MacLeod and Clarke, 2015). For example, the type of care-giving and the type of parental communication were found to be associated with children's performance on inhibition, WM, and cognitive flexibility tasks (Spruijt et al., 2018). Moreover, there is evidence that cognitive-behavioral and pharmacological treatments for anxiety also tend to reduce attentional biases to threat-related cues (Reinecke et al., 2013; Van Bockstaele et al., 2014). In light of the above, studies on adult interventions, such as cognitive training of adaptive allocation of attention or improvement of inhibitory functions, aim to reduce attentional biases. In non-clinical samples, attention modification has been shown to reduce distress, behavioral signs of anxiety, and intrusive thoughts elicited during subsequent exposure to cognitive stressors, public speaking challenges, and worry inductions in adults and children (Bar-Haim et al., 2011; MacLeod and Mathews, 2012).

There is also evidence for neural plasticity following training. For example, using a demanding task requiring inhibition of distracters, Cohen et al. (2016) trained healthy participants to exert cognitive control. One week of training resulted in reduced activation in the AMY when presented with threatening distracting pictures, which was linked to a reduction in emotional interference to task performance; furthermore, the training also resulted in enhanced PFC-AMY connectivity. Similarly, Beauchamp et al. (2016) employed an inhibitory control training task using a stop signal and showed that the training group exhibited reduced activity in prefrontal and supramarginal regions. Although, unlike the training by Cohen et al. (2016), this training did not result in behavioral changes, the neural changes were found in regions previously associated with motivation, expectancy, and executive attention, suggesting that the training was effective. In adult clinical samples, medium-to-small treatment effects have been observed compared to placebo training (MacLeod and Clarke, 2015; Price et al., 2016). The most promising and consistent effects have emerged in studies where the intervention showed evidence of "target engagement", that is, a demonstrable reduction in attentional biases to threat-related cues (MacLeod and Grafton, 2016; Price et al., 2016). Finally, important limitations of existing protocols for attentional bias modification have also been highlighted (see discussion in Okon-Singer, 2018). For example, it was noted that training may be efficient only for a certain age and when conducted in laboratory settings (Price et al., 2016; see also Koster et al., 2017 who noted that training efficiency depends on the fit between the type of training and diagnosis).

5.3. Attentional control and working memory training in anxiety and depression

Emerging research shows that in emotional disorders such as anxiety and depression, the balance between emotional and cognitive brain systems is disrupted and biased towards processing of negative emotional information (threat, sadness, etc.). Indeed, a major characteristic of anxious and depressed people is to process threatening information to large extents, ruminate on past negative events, and worry excessively about the uncertainty of the future (see Mogg and Bradley, 2018, for a review). Our brain systems are capacity limited, and so when we get stuck on negative (and task irrelevant) information, we have fewer resources to invest in completing the demands of the tasks at hand, and find it difficult to shift attention and process information efficiently (Derakshan and Eysenck, 2009). This gives rise to patterns of cognitive inflexibility (see Stange et al., 2017, for a review). When executive functions of WM become inefficient and rigid, we are more likely to distract from attending to the necessities of the task at hand, experience interference, and so find it difficult to achieve our goals efficiently (Berggren and Derakshan, 2013a).

5.3.1. Attentional control interventions in anxiety

According to the ACT of anxiety (Berggren and Derakshan, 2013a; Eysenck et al., 2007), as a result of impairments in processing efficiency and attentional control, the brain engages in recruiting extra cognitive resources for achieving behavioral outcomes; usually, referred to as compensatory effort, a prediction that has received much support to date (Ansari and Derakshan, 2011). ACT proposed a key central role for attentional control as a determinant of emotional vulnerability and resilience in anxiety, which may also hold for depression (De Raedt and Koster, 2010). The idea was that poor levels of attentional control (or cognitive inflexibility) can act as a risk marker for the onset, maintenance, and the recurrence of anxiety. Similarly, in depression attentional control has been argued to play a causal role in the development, maintenance, and recurrence of depressive states, with accumulating evidence supporting this (see Koster et al., 2017, for a review).

The thinking that attentional control can have a causal role to play in vulnerability to emotional disorders has received substantial support in a number of clinical (Motter et al., 2016) and educational (Holmes and Gathercole, 2014) domains. There are huge implications not only for treatment but also for preventing these disorders. Interventions can be built to exercise neuroplasticity in executive functions of WM targeting neural circuits involved in boosting attentional control. The idea is that, with better levels of attentional control, individuals can manage and regulate emotional experiences more effectively, feel empowered, improve performance levels, and boost immunity against vicious cycles of negative thinking, worrying, and helplessness, which are main features of anxiety and depressive states. Boosting attentional control and cognitive flexibility through neuroplasticity induced change holds much promise in psychopathology, where the exercise of key neurocognitive functions can be used to treat as well as protect against escalating levels of emotional vulnerability (Siegle et al., 2007a). Whilst still in their infancy, cognitive training interventions have shown promise in promoting neuroplasticity-induced change in main executive functions of WM towards improving attentional control. The exploitation of such techniques to improve our understanding of the causal role of attentional control in psychopathology has received substantial attention. At the same time, this also allows to examine the potential of such interventions to reduce emotional vulnerability levels in anxiety and depression. Findings dating back to work by Siegle and colleagues (Siegle et al., 2007b) show that it is possible to reduce depressive related symptomatology using cognitive training, with reductions in ruminative thinking being a key mediating mechanism (see also Hoorelbeke and Koster, 2017; Siegle et al., 2014).

A consistent finding across numerous studies shows that levels of engagement with the training, and improvement on the training task, correlates with reductions in emotional vulnerability (e.g., Grol et al., 2018; Hotton et al., 2018). Consequently, greater engagement levels with training are shown to predict lower levels of emotional vulnerability post vs. pre-intervention, at least in subclinical levels of emotional vulnerability to psychopathology. In an applied extension of this paradigm to target anxiety related impairments in practices such as tennis performance, where the exercise of attentional control is key to successful performance, the adaptive dual n-back training has improved tennis performance under situations of high pressure (anxiety), through its effects on increasing WM capacity (Ducrocq et al., 2017). In a novel application of the adaptive dual n-back training intervention to targeting emotional symptomatology in survivors of breast cancer, it was found that, compared to controls, participants who underwent the adaptive training protocol for two weeks showed marked reductions in anxiety and distress as well as rumination up to 18 months post intervention (Swainston and Derakshan, 2018). This was accompanied with self-reports of how much participants enjoyed the training and how it made them feel empowered and able. The fact that training helped reduce emotional vulnerability was important, because emotional vulnerability to anxiety and depression in this population is high, but the key finding was the sustainability of these reductions over time,

attesting to the consolidating effect of neuroplasticity induced changed over prefrontal regions.

The application of cognitive training techniques in clinical settings has been less investigated and should be a direction for future research to exploit. There is promising evidence that increasing processing efficiency via cognitive training targeting patterns of affective processing can help improve cognitive appraisal (Cohen and Mor, 2018) and emotion regulation (Hoorelbeke et al., 2016; Ritchey et al., 2011a; Schweizer et al., 2013), with significant implications for a number of populations at risk of anxiety and depressive disorders. In a similar fashion, if cognitive training has the potential to increase processing efficiency then it can aid in the efficacy of dominant therapeutic interventions, such as cognitive behavioral therapy and mindfulness, which rely on attentional control. A recent study found that, when the adaptive dual n-back training was combined with mindfulness meditation, it had the greatest longitudinal effects on reductions in trait worrying in a sample of high worriers, compared to when mindfulness was administered alone (Course-Choi et al., 2017). This suggests that the adaptive dual n-back through its emphasis on cognitive plasticity aided in the efficacy of mindfulness meditation which uses prefrontal functions of control.

5.3.2. Attentional control interventions in depression

The past decade, a number of studies have investigated different types of attention and executive training programs to remediate depressive symptoms and/or vulnerability to depression. Although this research area is still under full development, there are several interesting strands of research that we briefly discuss below. Based on the research that has indicated that depression is characterized by problems in disengaging attention from negative information, several studies have investigated whether retraining this attentional bias has positive effects on depressive symptoms. Based on the seminal studies on the influence of experimental manipulation of attentional bias on emotional reactivity (MacLeod et al., 2002), researchers have examined whether ABM is capable to influence emotion regulation and depressive symptoms, specifically. In ABM research, the standard dot probe task that is typically used to examine attentional bias is changed into a training task that is intended to manipulate attentional bias. Within this task, a pair of an emotional and a non-emotional stimulus are briefly presented on a screen, followed by a task-relevant probe that replaces one of these two stimuli. To manipulate attention towards or away from an emotional stimulus, this probe can be presented always at the location of the emotional or the non-emotional stimulus, encouraging attention to be deployed to emotional information or away from emotional information, respectively.

Initial studies using ABM training based on the dot probe task were suggestive of potential benefits of ABM in reducing depressive symptoms in subclinical depression (Wells and Beevers, 2010) and depression vulnerability in remitted depressed individuals (Browning et al., 2012). However, these effects were typically quite small and other studies failed to observe any effects of ABM on clinically depressed individuals (Baert et al., 2010). This lack of robust effects could be due to several reasons. For instance, it could be that visual attention is not of key relevance in depression, some of the trained stimulus material may not be as unambiguous as in anxiety (words like “happy” can be interpreted in different ways), or the dot probe is not very effective as an attention training procedure in general (see Koster and Bernstein, 2015). In recent years, authors have started to use eye-tracking methodology to retrain attentional bias in depression. For instance, Sanchez et al. (2016) monitored attention to positive and negative words during the unscrambling of ambiguous scrambled sentences (“life is my party a mess”). Here, attentional bias is first assessed by examining attention deployed to positive and negative words during unscrambling into grammatically correct sentences. Subsequently, participants are asked to always form positive sentences by deploying attention to the positive words. Individuals are assisted through online feedback about attention

deployment. This training has been shown to increase emotion regulation (positive appraisal). Other studies using similar strategies found that attentional bias can be modified in subclinically depressed individuals (Krejtz et al., 2018). Despite such encouraging findings, this field is in need of larger strictly controlled clinical trials.

In a largely independent line of research, it has been examined whether remediating more general cognitive control functions has beneficial effects on depressive symptoms. In this context, it is important that many researchers initially thought that cognitive impairments in depression are a byproduct of negative mood, not an important factor. However, views have changed markedly where cognitive/executive impairments can hamper daily activities and emotion regulation, and can contribute substantially to depression (Millan et al., 2012). Siegle and colleagues proposed that cognitive control training might be an important way to remediate some of the neurocognitive problems in depression, and they provided pilot data using an adaptive version of the Paced Auditory Serial Addition Task. In this task, participants are presented with a continuous stream of digits (several seconds apart) and are asked to add the last two heard digits. Upon successive correct responses the task goes faster. The task goes slower when consecutive errors are made. Several studies have applied this training in individuals at risk for depression (for instance remitted depressed individuals; Hoorelbeke and Koster, 2017), as well as in clinically depressed individuals (Siegle et al., 2014). Meta-analytic evidence (Motter et al., 2016) as well as a recent systematic review (Koster et al., 2017) indicate that this type of training can improve depressive symptoms, if sufficient training sessions are administered in individuals with pre-existing vulnerability to depression.

In recent years, a number of interesting developments have emerged in this area. First, authors have developed training procedures that include emotional information which could remediate valence-specific impairments in cognitive control (e.g., Daches et al., 2015). Second, initial work has started to elucidate the neural correlates of cognitive control training (Cohen et al., 2016). Finally, based on this neuroimaging work, researchers are increasingly studying the effects of combined interventions on depression, where the combination of cognitive control training and neurostimulation techniques (repetitive TMS) is considered promising (De Raedt, 2015). In an intervention that used the adaptive dual n-back training to target cognitive deficits in dysphoria (subclinical depression), neurocognitive mechanisms underlying WM capacity and filtering efficiency performance showed improvement after training (Owens et al., 2013). The adaptive dual n-back training intervention which was originally found to improve fluid intelligence, increased WM capacity and filtering efficiency of irrelevant information in dysphoria. This intervention is known for its challenging exercise of prefrontal functions, in a systematic and adaptive manner, with the active control participants engaging in a substantially less demanding non-adaptive version of the training. In a similar fashion, this training intervention was shown to be effective in enhancing resting state attentional control, as measured through electrophysiological measures, as well as inhibitory control, as measured by a flanker task, in high trait anxious individuals who trained on this task for 15 days over three weeks (Sari et al., 2016).

Despite the proven promise of the effectiveness of cognitive training techniques in influencing emotional vulnerability through enhancing attentional control, the field is still in its infancy and needs to grow to accommodate more precise and tailored training regimens for maximum benefit. Understanding the trajectory of neurocognitive change post intervention is key, because it can help build interventions that can produce more sustainable effects over time and enable change at a more fundamental level. Adopting a performance-based approach for examining neurocognitive improvements over time, as a result of training, and its potential impact on every day memory and cognitive functioning should be examined more thoroughly. Overall, targeting prefrontal functions of control and flexibility shows promise to improve every day well-being towards resilience. The flexibility to adjust and to

accommodate change in an optimum fashion according to situational demands requires effective practice and consolidation of neuroplasticity induced change. Whilst these theoretical ideas are robust, the methods are still in development. A multi-dimensional understanding of pathways of transfer-related change in explaining training effects is needed to optimize the efficacy of interventions and their external validity in other performance-related domains.

5.4. Focused attention training to optimize emotion processing and enhance well-being

Aside from the emotion control strategies discussed above, research has begun to elucidate the impact of emotion regulation strategies involving attentional deployment. One such strategy, focused attention (FA), involves shifts (controlled and deliberate, or instinctive and automatic) in attention to or away from the emotional aspects of emotion eliciting stimuli or (memory for) events, depending on the regulatory goal of the individual at that time (Gross, 2008; Sheppes et al., 2014). The effectiveness of attentional deployment emotion regulation strategies has been supported by a recent meta-analysis (Webb et al., 2012), and the underlying neural mechanisms have been also investigated (Denkova et al., 2013a, 2013b, 2015; Iordan et al., 2019). Attentional deployment strategies may be more efficient in controlling emotional responses, due to their faster deployment (Hajcak et al., 2009; Paul et al., 2013) and reduced cognitive demands (Mauss et al., 2007), compared other emotion regulation strategies such as reappraisal. Evidence shows that such strategies are deployed earlier in the emotion generation sequence (Hajcak et al., 2009; Paul et al., 2013), both when used with external stimuli (pictures) (Sheppes et al., 2014) and with recollected memories (Denkova et al., 2015). Moreover, FA has been also shown to be more effective when used during retrieval of AMs to reduce symptoms of depression (Kanske et al., 2012).

5.4.1. Focused attention and autobiographical recollection

Emotional AMs, such as the birth of a child, winning an award, or failing an exam, play an important role in the construction of personal identity, in future planning, and in decision-making. Hence, they are key factors in personal emotional well-being. In some circumstances, excessive focus on the emotional aspects of negative personal experiences can have debilitating consequences and lead to psychiatric disorders. To avoid such consequences, it is important to be able to control our emotional responses by switching our attentional focus away from the emotional aspects of our memories, and maintain healthy cognitive and affective functioning. Understanding how people deal with emotional AMs has relevance for understanding both normal healthy functioning and the dysfunction and negativity bias observed in patients with affective disorders. Indeed, excessive focus on emotional aspects of unpleasant memories has been associated with increased susceptibility to affective disorders, such as depression and PTSD (Rubin et al., 2008, 2011), which are characterized by impaired emotion regulation (Gotlib and Joormann, 2010; Mayberg, 1997). Recently the topic of emotion regulation has gained considerable interest, as the ability to cope adaptively with emotionally challenging situations is vital for physical and mental health, and understanding its mechanisms has important implications for understanding and treating affective disorders (Gross, 2008; Ochsner and Gross, 2005).

Recent evidence highlights the effectiveness of short-term training of FA with AM retrieval, both in isolation and in the context of a dual task with AM recollection presented as *internal* emotional distraction (Denkova et al., 2013a, 2013b, 2015; Iordan et al., 2019). For example, Denkova et al. (Denkova et al., 2013a, Denkova et al., 2013b, 2015) showed that focusing attention on the non-emotional contextual aspects (such as time, location, other people present) of highly emotional personal memories, and away from the emotional aspects, was associated with lower self-reported emotional responses, increased activity in the ventromedial PFC (vmPFC), and decreased activity in the AMY.

Moreover, a mediation analysis suggested a role of the vmPFC in integrating affective signals from the AMY and mediating their impact on the subjective re-experiencing of emotion, according to the current retrieval/attentional focus. While these findings refer to both pleasant and unpleasant AMs, valence-related differences were also identified in the PFC and MTL (Denkova et al., 2013a, 2013b). Importantly, the finding regarding the role of the AMY described above (see also Dolcos and McCarthy, 2006) challenges evidence from previous emotion regulation studies (Johnstone et al., 2007; Urry et al., 2006), mainly emphasizing top-down influences on AMY activity from the PFC regions involved in cognitive control, rather than reciprocal AMY-PFC influences, initiated in the AMY. In addition, FA is also effective in reducing the impact of recollected unpleasant AMs when triggered as internal emotional distraction during a WM task (Iordan et al., 2019). Behaviorally, focusing away from emotional aspects of AMs was associated with better WM performance than focusing on the recollected emotions. Additionally, when participants focused on non-emotional contextual details of their memories, there were reduced responses in brain regions associated with the salience network (i.e., AMY, dorsal ACC, anterior insula), coupled with greater recruitment of executive prefrontal (dlPFC) and memory-related temporoparietal regions (parahippocampal gyrus, angular gyrus), along with increased fronto-parietal connectivity. Additionally, temporal dissociations were identified between regions involved in self-referential (showing faster responses) versus context-related processing (showing delayed responses).

It is important to note that such manipulations following short training in using FA with AM recollection can be linked to emerging evidence regarding the effect of *episodic specificity induction* – i.e., brief training in recollecting episodic details (Madore and Schacter, 2016). Research on episodic specificity induction has revealed that focusing on very specific episodic details of recent events can enhance subsequent performance on a range of cognitive tasks (Madore et al., 2015; McFarland et al., 2017), and also psychological well-being (Jing et al., 2016). These findings are also consistent with recent evidence showing that training to recollect AMs with increased specificity may yield beneficial effects in depression (Watkins et al., 2009). The findings from the Denkova et al. (2015) and Iordan et al. (2019) studies extend such investigations to emotional AMs, by showing that focusing on non-emotional aspects of AMs can influence the emotional (re)experience of such memories. In sum, attentional deployment strategies, such as FA, seem to have beneficial effects on retrieval of emotional personal memories, because they can enhance the emotional impact of positive memories and reduce the impact of negative ones. These behavioral effects are coupled with differential recruitment and connectivity among PFC (lateral and medial) and MTL (AMY and HC) regions. Together, these findings support the idea that laboratory tasks can also be expanded into long-term interventions to train behaviors and brain responses for improved emotion-attention interactions.

5.4.2. Focused attention and long-term mindfulness training

In recent years, there has been growing interest in the use of FA training and intervention programs to improve emotion-attention interactions and to identify the underlying brain mechanisms associated with such improvements (Fox et al., 2014; Lomas et al., 2015). Laboratory tasks involving manipulations and trainings of attention have been diverse. Some common forms of attention training include the dot-probe, visual search, and clinical auditory tasks, which involve visual or auditory manipulations of attention often with the goal of distracting from negative information and engaging neutral or positive information (Wadlinger and Isaacowitz, 2011). One form of FA intervention that has gained particular prominence is *mindfulness*, which generally refers to “the awareness that emerges through paying attention on purpose, in the present moment, and non-judgmentally to the unfolding of experience moment by moment” (Kabat-Zinn, 2003). Additionally, similar meditation-oriented interventions, and some lab tasks, have also shown promise (e.g., integrative body-mind training, Tang and Posner, 2009).

Training programs focusing on mindfulness typically target skills aimed at reducing distressing symptoms, including those associated with psychological disorders and somatic conditions. Emerging work suggests that focused attention interventions can modulate memory encoding and retrieval (Erisman and Roemer, 2010; Roberts-Wolfe et al., 2012), which has important implications for affective disturbances where emotional dysregulation and emotional memories may be a factor contributing to the reduction of overall well-being (e.g., PTSD, depression). At the time of encoding, for example, a brief mindfulness intervention has been shown to enhance reported positive affect in response to a positive film clip and to reduce reported negative affect following an affectively mixed film clip (Erisman and Roemer, 2010). Consistent with these findings, another recent study showed that a group instructed in focused breathing, one strategy for mindfulness training, maintained positive responses to neutral images before and after training, while unfocused attention and worry groups responded more negatively to the neutral images after the instructed session than before it (Arch and Craske, 2006). At the time of retrieval, mindfulness practitioners appear to show greater increases in positive word recall compared to controls (Roberts-Wolfe et al., 2012), or lower proportions of negative word recall (Alberts and Thewissen, 2011). Mindfulness interventions also appear to increase AM specificity, and decrease memory overgeneralization, which are common symptoms of depression (Heeren et al., 2009; Williams et al., 2007).

At the neural level, mindfulness interventions have been shown to induce changes in both the structure and function of the brain, including structures involved in attention, emotion, and memory. For example, studies of brain structure have associated mindfulness training with increased gray matter volume or density in the cingulate cortex (Hölzel et al., 2011), insula (Murakami et al., 2012), and HC (Hölzel et al., 2011). Evidence for structural changes in the AMY seems a bit less clear (Hölzel et al., 2010; Murakami et al., 2012), and is perhaps influenced by other factors such as sample demographics. However, in general, available evidence appears consistent with the idea that mindfulness engages brain regions that are key for body awareness, memory, and emotion (Fox et al., 2014). Mindfulness and meditation practice have also been linked to modulation of structural connectivity between brain regions. For example, meditation practice has been associated with changes suggesting enhanced connectivity within and between hemispheres of the brain (Luders et al., 2012; Tang et al., 2010), which is in line with the idea that mindfulness and meditation training can improve the underlying connections in the brain that support attentional self-regulation processes (Luders et al., 2012). At the functional level, mindfulness training was linked to changes in the intrinsic functional connectivity between the default mode and salience networks (Doll et al., 2015), consistent with the idea that interactions between brain networks support the ability to attend to current experience without judgment. Moreover, mindfulness training appears to also influence brain activity when engaged in tasks, such as paradigms that involve responding/regulating responses to emotional stimuli. A study by Creswell and colleagues (Creswell et al., 2007), for instance, showed that when labeling emotions, the AMY was negatively associated with lateral PFC activation in more mindful individuals. This evidence is consistent with the idea that mindfulness training modulates the neural mechanisms involved in emotion processing.

Although how FA interventions alter brain structure is still an open question that is being investigated, a number of possible mechanisms have been proposed (reviewed in Tang et al., 2015). An account referred to as “use-dependent plasticity” (for reviews of relevant studies in humans, see Draganski and May, 2008; May, 2011) suggests that there is a relation between the structure of the brain and its level of use. This account may describe a result of Hebbian learning (Hebb, 1949), and suggests that these structural changes might lead to alteration in brain structure (Draganski et al., 2006). Consistent with the Hebbian learning model, it is possible that repeated engagement in FA affects

brain structure through expansions of existing synapses and dendrites, or creation of new synapses. It is also possible that engaging in FA induces the formation of new neurons or myelin sheaths that help insulate the connections between neurons. Another possibility is that FA influences autonomic and immune activity, which might help preserve or restore neurons. Alterations in these mechanisms at the level of brain cells might contribute to overall changes in the volume of brain regions and the integrity of the connections between them.

In sum, FA manipulations and interventions, such as mindfulness training, seem to have beneficial effects on encoding and retrieval of emotional memories, because they can enhance the emotional impact of positive memories and reduce the impact of negative ones, and improve overall well-being. Regarding the neural correlates, available evidence points to down-regulation of emotion-sensitive brain regions (AMY) by the engagement of cognitive and attentional control regions (frontal and parietal cortices), similar to other emotion regulation strategies, such as reappraisal (Kanske et al., 2011; McRae et al., 2010). Further research in this area will continue refining our understanding of these effective practices and associated neural mechanisms, in order to promote well-being.

6. Linguistics

With this understanding of the current state of research on emotion-attention interactions as a basis, our team was asked to review words used to express feelings related to attention. As described in the Introduction, within the realm of affective research, confusion arises over the fact that feelings are components of more complex affective responses. For example, “fear” as basic emotion consists of a continuum of automatically activated defense behaviors (Kozłowska et al., 2015) that co-occur with “feelings of fear.” Consequently, the term *feeling* is often used incorrectly as a synonym for *emotion* and vice versa (LeDoux, 2015; Munezero et al., 2014). But feelings are not emotions *per se* (LeDoux, 2015) and are not limited to those that co-occur with specific basic emotions. Rather, feelings might encompass a wide range of mental experiences, such as signifying physiological needs (e.g., hunger), tissue injury (e.g., pain), optimal function (e.g., well-being), the dynamics of social interactions (e.g., gratitude) (Damasio and Carvalho, 2013). Additional challenges relate to the fact that feelings are not consistently defined, and that definitions for these terms can evolve over time (Tissari, 2016). Moreover, while some feelings may be universally experienced across cultures (e.g., hunger, pain, cold, fatigue), others are understood to be culturally constructed (e.g., gratitude, optimism) (Boiger and Mesquita, 2012; Joshi and Carter, 2013).

As a result, the Human Affectome Project taskforce agreed that any attempt to create a linguistic inventory of articulated feelings would need to first define feelings in a manner that can help us understand the full range of terms to be considered and then undertaken with an acute awareness that variations in terminology are going to exist in day-to-day usage, between languages and across cultures. Hence, a definition for feelings was developed as part of the project. A small task team within the larger effort reviewed the literature to create a definition for feelings that could serve as a starting point. The task team produced a first draft and shared it with the entire taskforce of nearly 200 researchers, feedback/input was gathered, and then it was refined, re-distributed and the process iterated several times to achieve broad consensus within the group. The resulting definition is as follows:

A “feeling” is a fundamental construct in the behavioral and neurobiological sciences encompassing a wide range of mental phenomena and individual experiences, many of which relate to homeostatic aspects of survival and life regulation (Buck, 1985; Damasio and Carvalho, 2013; LeDoux, 2012; Panksepp, 2010; Strigo and Craig, 2016). A broad definition for feeling is an appraisal or mental representation that emerges from physiological/bodily states (Damasio and Carvalho, 2013; LeDoux, 2012; Nummenmaa et al., 2014), processes inside (e.g., psychological processes) and outside the central

nervous system, and/or environmental circumstances. However, the full range of feelings is diverse as they can emerge from basic emotions (Buck, 1985; Damasio and Carvalho, 2013; Panksepp, 2010), levels of arousal, actions (Bernroider and Panksepp, 2011; Gardiner, 2015), hedonics (pleasure and pain) (Buck, 1985; Damasio and Carvalho, 2013; LeDoux, 2012; Panksepp, 2010), drives (Alcaro and Panksepp, 2011), and cognitions (including appraisals of self) (Ellemers, 2012; Frewen et al., 2013; Northoff et al., 2009), motives (Higgins and Pittman, 2008), social interactions (Damasio and Carvalho, 2013; Gilam and Hendler, 2016; LeDoux, 2012; Panksepp, 2010), and both reflective (Holland and Kensinger, 2010) and anticipatory perspectives (Buck, 1985; Miloyan and Suddendorf, 2015).

The duration of feelings can vary considerably, from those associated with brief emotional responses (surprise) to longer-lasting sentiments (love). They are often represented in language (Kircanski et al., 2012), although they can sometimes be difficult to recognize and verbalize, and some feelings can be shaped by culture (Immordino-Yang et al., 2014). Feelings that are adaptive in nature (Izard, 2007; Strigo and Craig, 2016) serve as a response to help an individual interpret, detect changes in, and make sense of their circumstances at any given point in time. This includes homeostatic feelings that influence other physiological or mental states, emotions, motives, actions, and behaviors in support of adaptation and well-being (Damasio and Carvalho, 2013; Strigo and Craig, 2016). However, some feelings can be maladaptive and may compete and/or interfere with goal-directed behavior.

Finally, as also mentioned in the Introduction, a “feeling” is not a synonym of “emotion.” Also, there is standing debate between researchers who posit that discrete emotion categories correspond to distinct brain regions (Izard, 2010) and those who argue that discrete emotion categories are constructed of generalized brain networks that are not specific to those categories (Lindquist et al., 2012). However, both groups acknowledge that in many instances feelings are discernable components of emotional responses, which tend to be more complex.

Using this definition of feelings as a starting point, the linguistics task team then undertook a formal linguistic analysis and ultimately proposed nine broad categories of feelings (i.e., Physiological or Bodily states, Attraction and Repulsion, Attention, Social, Actions and Prospects, Hedonics, Anger, General Wellbeing, and Other) (Siddharthan et al., 2018). Feelings related to attention were described as “Feelings related to focus, attention, or interest (e.g. *interested*, *curious*, etc.), or the lack thereof (e.g. *uninterested*, *apathetic*, etc.).” We reviewed the feelings found in this category of this linguistics analysis, consisting of just 51 meanings that fell into a handful of categories. Several terms related to the degree of interest, ranging from uninterested and inattentive at one extreme to conscious awareness, attentive, and engrossed at the other extreme. Other categories of meanings that we could discern referred to *social attentiveness*, and indexing possible causes of attention, such as *curiosity* and *fascination*. Lastly, one set of meanings referred to attention when it is directed towards inner thoughts (e.g., *meditative*, *pensive*) (see Supplementary Table 1 for details).

It is interesting to note that the feelings ranging from uninterested and inattentive at one extreme to conscious awareness, attentive and engrossed at the other extreme represent a continuum along the valence and arousal dimensions, from negative valence, low arousal word meanings that extend to positive valence, high arousal meanings. However, there are notable exceptions, as some words may be highly arousing and negatively-valence, such as “obsessed.” At the same time, some “feeling” words related to attention directed towards inner thoughts do not appear to be valenced; instead, they primarily represent a statement of attentional status, which is notable since most feelings are assumed to be valenced.

7. Conclusions and future directions

The present review provided a survey of available and emerging evidence on emotion-attention interactions and the associated neural mechanisms, capitalizing on contributions from researchers with diverse expertise spanning behavioral, lesion, brain imaging, and intervention approaches. We began by discussing available evidence concerning how emotion-attention interactions influence basic perception and social cognition (section 2), as well as learning and different types of memory (working and episodic) (section 3). Then, we turned to our discussion of the role of individual differences in a variety of domains that affect emotion-attention interactions (section 4). Finally, we discussed emerging evidence demonstrating how training and interventions can optimize emotion-attention interactions (section 5). The themes from these sections are also reflected in the terms identified by the linguistic search (section 6) that is central to this special issue (see Supplementary Table 1), including domains related to conscious awareness, motivational effects of attention, social attention, and emotion regulation. This comprehensive approach allowed for an integrative overview of the available evidence regarding the mechanisms of emotion-attention interactions and highlighted emerging directions for future investigations. Consistent with the framework described in the Introduction, we will briefly summarize and discuss the extant evidence in the context of these core themes.

7.1. Emotion-attention interactions in perception

The available evidence on emotion-attention interactions addresses many aspects related to perception, spanning from whether processing of emotional information can occur without conscious awareness to how emotion-attention interactions are associated with processing of higher-order social cognition. Although controversy still exists, evidence suggests that processing of emotional information in humans can occur without awareness, and highlights the AMY as playing a key role, whereas evidence regarding cortical emotion processing regions (i.e., mPFC and vIPFC) points to susceptibility to modulation by attention when attentional resources are most available (Shafer and Dolcos, 2012). This recent research also highlights the importance of whether emotional stimuli are task-relevant and enhance cognitive performance, or are task-irrelevant and impair performance. Much of the research on emotion-attention interactions has focused on negative emotion, but a growing corpus of evidence has shown that incentives or positive reinforcement (i.e., gaining monetary or other forms of reward for correct performance) can improve performance on cognitive tasks. Similar to negative emotional stimuli, presentation of stimuli associated with reward or signaling potential future reward or loss of reward can contribute to distraction, if such reward signals are incongruent with the current task (Anderson et al., 2013). Neuroimaging and physiological evidence suggest that reward stimuli recruit attentional resources, and shape motor selection and action via interactions among the ventral striatum, dorsal striatum, and prefrontal cortex (Braver, 2016; Pessoa, 2013).

Evidence also highlights emotion-attention interactions in the context of social cognition, both at the level of initial perceptual processes and attention paid to social stimuli, such as faces, bodies, and voices (de Gelder, 2006; Grandjean et al., 2005), and at the level of higher-order social cognitive processes (Freeman and Ambady, 2011), such as impressions, judgements, and decisions. At the level of perception, research has largely examined processing of faces, and more recently bodies, and the association with electrophysiological (ERP) and hemodynamic (fMRI) markers. In the ERP domain, the N170 component was delayed but enhanced for both inverted faces and bodies (Stekelenburg and de Gelder, 2004). In the fMRI domain, both body- and body parts-specific areas have been identified in the FG, between face sensitive clusters in the FBA, and in the lateral occipital cortex, termed EBA (Downing et al., 2001; Peelen and Downing, 2007).

In the context of higher-order perception in social cognitive processes, such as interacting with unknown others for whom no relevant information is available, people rely on a variety of factors, such as physical appearance, verbal behavior (Ames et al., 2011), as well as subtle nonverbal behavior, or affective body language (de Gelder et al., 2010), as cues to form an impression. Moreover, recent studies show that the neural network engaged during dynamic whole body perception and interaction involves the AMY, FG, pSTS, and the mPFC (Dolcos et al., 2012; Katsumi and Dolcos, 2018). During these interactions, individuals might perceive and respond to cues that indicate *approach* and *avoidance* motivations, namely, to seek out a given object or activity, or to escape from the object or activity, respectively (Braver et al., 2014; Elliot et al., 2013). A recent model proposes that there are dynamic interactions between bottom-up signals (facial, vocal, and bodily cues) and top-down factors (stereotypes and prior knowledge) that lead to unified perceptions and responses to others (Freeman and Ambady, 2011). The kinds of information processed in the model include cue level inputs (i.e., face, body, and voice cues), category level factors (i.e., sex, race, age, emotion), stereotypes level factors, and high level cognitive states, highlighting the interactions that can occur among these factors.

Open questions also remain in several key aspects in the area of emotion-attention-perception interactions, where additional research is needed to clarify these phenomena and their neural correlates. For example, future research is needed to clarify the link between AMY engagement and the early time course for the processing of emotional stimuli under conditions of conscious and unconscious viewing, and the types of emotional stimuli that can be processed without awareness. Additional research should also target the extent to which attentional load modulates neural activation in subcortical regions supporting processing of salient information, such as reward. Finally, further research is needed to elucidate the interactions of the complex number of factors that influence social cognition/evaluation, to refine emerging models and the implications for conditions where social-emotional functioning is impaired, such as autism and social phobia (Gilboa-Schechtman et al., 1999; Mazefsky et al., 2012).

7.2. Emotion-attention interactions in learning and memory

Evidence also highlights emotion-attention interactions in short- and long-term forms of memory, linked to working and episodic memory. The former closely relates to selective attention processes and, in the context of affective WM, available evidence points to reliable neural recruitment of the VAS, although the behavioral effects are more mixed. In the context of emotional distraction and WM, studies investigating the neural correlates of the basic response to emotional distraction point to an interplay between two major neural systems: VAS, associated with emotional processing, showing increased activity, and DES, associated with executive processing, showing decreased activity (Dolcos and McCarthy, 2006). The impact of task-irrelevant emotional distraction is largely supported by bottom-up mechanisms that may redirect processing resources away from the main cognitive task and toward stimuli with enhanced relevance for survival.

In the context of longer-lasting effects following emotion-attention interactions, such as emotional episodic memory, the available evidence supports the notion that arousal and valence effects can be dissociated in the neural correlates of the memory-enhancing effect of emotion. Specifically, the MTL-based memory mechanism is relatively more involved in arousal-dependent effects, while the valence-related effects are linked to connectivity of these regions within the MTL as well as with regions such as the PFC and other cortical areas (e.g., parietal) (Dolcos et al., 2004a; Kensinger and Schacter, 2006). The latter appear to be relatively more sensitive to processing of valence and engage in higher order processes (e.g., semantic and WM, attention, cognitive control, and self-referential processing). Furthermore, ERP encoding results suggest that, under limited capacity for neural

representations (Bundesen et al., 2005), the set of processes involved in memory encoding prioritizes resources towards emotionally arousing and relevant information, at the cost of neutral non-relevant information (Watts et al., 2014; see for a review Mather and Sutherland, 2011). In turn, this leads to better memory formation for both emotional items and their associated source information. The response to acute stressors also interacts with processes such as attention, learning, and memory. Acute stress quickly promotes hypervigilance states via the activation of the salience network (Hermans et al., 2014) that entails the co-activation of the AMY, the dorsal ACC, hypothalamus, the anterior insula, the striatum, the thalamus and inferotemporal and temporoparietal regions (Corbetta et al., 2008), but the network downregulates with the passing of time, reducing the sustained attention back to normal levels. Delayed effects of stress modulators, such as genomic glucocorticoids, appear to play an important role in adapting response (Hermans et al., 2014; Joëls et al., 2011).

Open questions in the area of emotion-attention interactions in learning and memory also exist. For instance, future research is needed to clarify the association between affective WM paradigms used in the laboratory and affective WM capacity in real world environments (e.g., Pe et al., 2013a). It is also unclear the link between the immediate and long-term effects in the impact of emotional distraction on working and episodic memory respectively. Finally, additional research is also needed to further probe the interaction of the catecholamines and glucocorticoids that mediate both initial and subsequent stages of processing influencing learning and memory, through pharmacological interventions or new neuro-stimulation methods (transcutaneous vagal nerve stimulation, Van Leusden et al., 2015; Ventura-Bort et al., 2018).

7.3. Individual differences in emotion-attention interactions

It is also important to consider the various ways in which individual differences (sex, developmental, personality) can modulate emotion-attention interactions in both healthy functioning and clinical conditions. For example, evidence highlights differential sensitivity to basic affective properties across the lifespan and between females and males. Although females generally exhibit enhanced emotional competence in emotion processing, compared to males, they are also more likely to show a negative affective bias in attention and perception, enhanced emotional distractibility and memory, as well as differential engagement and lateralization of the AMY during emotional memory encoding and consolidation. Developmentally, whereas children tend to show greater interference by emotional distracters compared to adolescents and adults, and enhanced memory for emotional compared to neutral events (Somerville et al., 2011; Tottenham et al., 2011), older adults tend to show reduced distraction by negative emotional stimuli and greater susceptibility to the memory trade-off effect between emotional/central vs. non-emotional/peripheral aspects of an event, compared to young adults (Kensinger et al., 2007; Mather, 2012). At the neural level, children tend to show greater AMY activation along with more wide-spread activation during the encoding of emotional information (Nelson et al., 2003; Vasa et al., 2011). Older adults tend to show decreased AMY response to negative stimuli and increased AMY response to positive stimuli, along with increased engagement of the PFC and ACC regions during the encoding of negative vs. neutral and positive vs. negative stimuli (Dolcos et al., 2014; Mather et al., 2004; Nishiro et al., 2012; St Jacques et al., 2010).

Personality differences, such as trait anxiety and depression, also appear to play a role in the interaction between emotion and selective attention and control processes. For example, across a range of selective attention measures, anxious individuals show increased distractibility by task-irrelevant stimuli, suggesting impaired inhibition ability (e.g., Berggren and Derakshan, 2013b, 2014; Moser et al., 2012). Furthermore, attentional control is disrupted in high anxiety, while emotional processing appears to be enhanced, particularly in relation to threat. In the case of depression, emotional interactions with attention appear to

more generally encompass attentional biases to negative information than the relatively threat-specific idiosyncrasies of anxiety. Neuroscientific evidence targeting anxiety and depression suggest a trade-off between the engagement of prefrontal brain regions associated with attentional control versus relatively enhanced response within the limbic network related to negative stimuli (e.g., Davidson et al., 2002).

Prolonged or chronic alterations in affective and cognitive processing are commonly observed as symptoms of affective conditions (e.g., anxiety, depression, and PTSD), often reflected in altered emotional reactivity and recollection of emotional memories, along with impaired cognitive/executive control (Rauch et al., 2006; Shin and Liberzon, 2009). In the case of anxiety, findings indicate that alterations in attentional processes to emotion (i.e., threat-related stimuli) may have early-developing neural underpinnings. In the case of depression, findings suggest that individuals with depression or at familial risk of depression exhibit attentional biases toward negative emotion information (e.g., sad faces) and away from positive emotional information, and such responses seem to also be associated with alterations in fronto-limbic systems. Regarding PTSD, emotion regulation deficits are commonly observed (e.g., Ehling and Quack, 2010; Powers et al., 2015) and emotion regulation capacity predicts the onset and maintenance of post-traumatic stress symptoms following trauma (Jenness et al., 2016; Punamäki et al., 2015). Finally, available evidence from investigations of PTSD also points to chronic general and specific emotional and cognitive disturbances that are linked to alterations in the neural responses underlying emotion-cognition interactions, and specifically linked to attention. In particular, evidence suggests that reduction of AMY and HC signals for trauma-related cues may underlie non-specific encoding of gist-based representations instead of specific and detailed contextual details of the trauma-related memories. This, in turn, may be linked to symptoms of hypervigilance and non-specific responses to trauma-related distraction, which contribute to the maintenance of a hyperarousal state.

A number of open questions also emerge in the area of individual differences in emotion-attention interactions. For example, future research is needed to clarify whether evidence of reduced attentional control in anxiety can explain why these individuals also show enhanced biases to threat-related information, and the extent to which attentional control training can reduce anxious symptomatology. Additionally, future research is needed with longitudinal designs to determine how fronto-limbic systems supporting interactions between attention and emotion develop, and whether alterations in the development of these systems could contribute to the onset and maintenance of anxiety and depression.

7.4. Training and interventions to optimize emotion-attention interactions

Available and emerging research findings also highlight various ways in which attentional control, WM, and emotion regulation can be engaged or trained in intervention approaches. For example, common emotion regulation processes range from attentional control to cognitive change. The former refers to attention selection toward or away from affective information depending on its motivational properties, and the later encompasses the application of higher cognitive abilities including WM and long-term memory to emotion regulatory processes. Interestingly, both explicit and implicit emotion regulation appear to vary as a function of individual differences in executive control capacity. The neural correlates of successful emotion regulation include the lateral/medial PFC and dorsal ACC for implicit emotion regulation.

Another form of intervention is executive control training, which can refer to training involving cognitive processes such as WM and selective attention, necessary for controlling behavior. For example, attentional control and WM training has been a strategy for improving emotion-attention interactions in the context of anxiety. The idea that attentional control can have a causal role to play in vulnerability to emotional disorders like anxiety and depression has received

substantial support in a number of clinical (see Keshavan et al., 2014; Motter et al., 2016, for reviews) and educational (Holmes and Gathercole, 2014) domains. Additionally, evidence consistently shows that levels of engagement with the training, and improvement on the training task, correlates with reductions in emotional vulnerability (e.g., Grol et al., 2018; Hotton et al., 2018). Importantly, a recent review of different cognitive control trainings by Koster et al. (2017) concluded that, depending on the fit between type of training and diagnosis, training can (or cannot) improve emotion control and alleviate maladaptive emotional reactions among healthy controls and individuals diagnosed with depression. Attentional deployment strategies, such as FA, have also begun to be integrated into intervention approaches. Such strategies seem to have beneficial effects on encoding and retrieval of emotional memories, because they can enhance the emotional impact of positive memories and reduce the impact of negative ones. These effects appear to be associated with differential recruitment and connectivity among PFC (lateral and medial) and MTL (AMY and HC) regions. Other novel interventions targeting regulatory focus (Strauman et al., 2015) and combining state-of-the-art brain imaging methods, such as fMRI-guided neuronavigation, to individualize repetitive transcranial magnetic stimulation treatment for depression (Luber et al., 2017), are also helping translate brain imaging findings to improve therapeutic efficacy.

Importantly, much of the research on training and interventions highlighted here has been very recent, and hence there are still several key areas for further research. As with other training domains, while there is important promise of the effectiveness in influencing emotional vulnerability, the field is still in its early stages and needs to grow to accommodate more precise and tailored training regimens for maximum benefits. For instance, future research is needed to further clarify the association between explicit emotion regulation and executive control, in general, and WM, in particular. Additional research is also needed to further elucidate the effectiveness of cognitive training techniques in clinical settings.

7.5. Linguistic integrations

Notably, core aspects of emotion-attention interactions that emerge throughout the literature highlighted in this review are integrated with the terms identified by the linguistic analysis of words people use to convey feelings related to attention. Although the term “emotion” is often used in a broad way referring to a range of affective constructs, there are also specific and related aspects that can be differentiated when examining the terms describing feelings related to attention. For example, valence and arousal emerge as affective qualities that clearly influence attention and are evident in the identified terms. These dimensions can be seen in terms ranging from negative valence, low arousal categories, such as *inattentive*, to positive valence, high arousal categories such as *alert/attentive* and *engrossed*. Indeed, arousal and valence play an important role in emotion-attention interactions in the context of perception as well as in learning and memory, as shown by the extensive literature that has used stimuli such as emotion-eliciting images that are carefully controlled to be highly arousing and highly negative in valence (e.g., Lang et al., 2008). Motivation also emerges as an aspect that is related to processes involving reward and social cognition, and is highlighted by word categories relating to concepts including social attentiveness. For example, the literature on emotion-attention interactions in the context of higher-order social cognition points to processes in which individuals form impressions which could be influenced by social attentiveness (e.g., *chivalrous*). Additionally, attentional processes are highlighted by word meanings such as *attentive*, *conscious awareness*, *fascinated*, and *focused on inner thoughts*. Moreover, maladaptive emotion-attention interactions can be symptoms of affective disorders (e.g., *preoccupied*, *pensive/ruminative*), whereas training adaptive emotion-attention interactions is often a strategy for increasing resilience against, or decreasing symptoms of,

affective disorders (e.g., *mindful*, *meditative*).

In sum, we have reviewed current research and emerging directions in emotion-attention interactions, focusing on the associated neural mechanisms as revealed by functional brain imaging and physiological investigations. Such a comprehensive approach allowed for an integrative overview of the available evidence regarding the mechanisms of emotion-attention interactions and highlighted emerging directions for future investigations. As the field continues to address these issues, new findings will help to better clarify the dynamics and neural correlates of emotion-attention interactions and inform new and comprehensive models of the related psychological phenomena and brain functions. Overall, emerging and future research in these areas will continue refining our understanding of the effective practices and associated neural mechanisms, in order to better promote and maintain well-being.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2019.08.017>.

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